FURTHER STUDIES OF YUCCAS AND THEIR POLLINATION.

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Among the many strange things brought to light by biological studies, few equal in interest or verge so closely on the improbable as those which concern the pollination of the Yuccas. The observed facts, chiefly known through the work of Professor Charles V. Riley and the late Dr. George Engelmann, have been admirably summarized by Professor Riley in the Third Report of the Garden.* So far as direct observation on pollination is concerned, these refer to cultivated specimens of *Y. filamentosa* and *glauca*, the latter of which has been observed also in the wild state in Colorado; † but the collections of entomologists, and the affected fruits of the Yuccas of various localities, show that virtually all species of the genus depend for their principal pollination, if not altogether, upon moths of the Tineid genus Pronuba, of which Riley has characterized three species.‡ Professor Riley, therefore, states that all of the species of Yucca native east of the Rocky Mountains depend for their pollination, so far as is now known, upon a single species of Pronuba, namely the white *P. yuccasella*,§ while the tree Yucca of the California desert and the adjacent region, *Y. brevifolia*, is pollinated by a dingy moth, *P. synthetica*,‖ and the aberrant *Yucca Whipplei*, which Mr. Baker is now disposed to place in a distinct genus under the name Hesperoyucca, is pollinated by an equally aberrant spotted moth, *P. maculata*,¶ the pollinating actions of which have been briefly reported this season by Coquillet.** Aside from this

* pp. 99 to 158, pl. 34 to 43. † Riley, *l. c.* 124. ‡ *l. c.* 137.

§ *l. c.* 104, 121; Proc. Biological Society of Washington, vii. 94; Insect Life, iv. 369. ‖ *l. c.* 121, 141. ¶ *l. c*, 121, 139.

** Insect Life, iv. 370, note.

nothing definite has been made known concerning either the Pronubas which frequent the several species of Yucca, or their mode of operation, although Riley predicts the probable discovery of distinct species of Pronuba for the Mexican *Y. filifera** and our own *Y. rupicola*,† *Y. Treculeana*,† and *Y. baccata*.‡

The following pages contain the results of a further field study which I have been enabled to make during the spring of 1892, through the interest of the Board of Trustees of the Garden. In bringing the observations together, they have been arranged under the respective species studied, the classification of the latter being substantially that employed in the detail illustrations of the last volume. §

YUCCA.

Filaments nearly or quite free from the petals; pollen powdery; style stout, not capitately expanded nor long-papillate, with a rather open stigmatic axile canal; fruit baccate, spongy, or capsular with septicidal and apical-loculicidal dehiscence.

A. SARCOYUCCA, *with fleshy fruits.*

Y. ALOIFOLIA, L. (Pl. 18).—According to Riley,‖ individuals of this species which bloom simultaneously with *Y. filamentosa* along the southeastern coast, are pollinated by *Pronuba yuccasella*. The species is, however, quite unique in setting good fruit rather abundantly in cultivation when Pronuba does not appear to be present.¶ This was the case in the Garden this year, when the species

* *l. c.* 121. † *l. c.* 122. ‡ Proc. Biol. Soc. Washn. vii. 96.

§ Third Report Mo. Bot. Garden, 161. ‖ *l. c.* 121.

¶ The principal references to the fruiting of *aloifolia* without Pronuba are the following: Deleuil, Rev. Horticole. — abst. in Gard. Chron. 1880, xiii. 807; Engelmann, Gard. Chron. 1872, 941, Collected Writings, 284; The Garden, *fide* Vick's Mag. 1880 and Riley in Proc. Amer. Ass. Adv. Sci. xxix. 624; Gardeners' Chronicle, 1880, xiii. 81; Riley, Third Garden Report, 118 etc.; J. v. V. [van Volxem], Gard. Chron. 1882, xviii. 407. The note of Layard in Nature, xxii. 606, may perhaps refer to this species, though the species is not named.

bloomed for the first time in several seasons, and a number of the panicles fruited quite freely. The earliest of these flowers opened as the last flowers of *filamentosa* were falling, so that it was supposed at first that they were pollinated by *P. yuccasella*, which had been observed only a few days previously, but this supposition was not substantiated by the discovery of the moth about them, or of its larvæ in the fruit.

Professor Riley has shown that the short style and open stigma of *aloifolia* appear to favor self-pollination when the moth is not present; but a study of our plants this summer by Mr. Webber and myself has not satisfied either of us that self pollination is likely to occur sufficiently frequently to explain the rather abundant fruiting observed here, and in the case of a single panicle covered with gauze, no fruit was set except as the result of artificial pollination. The so-called Yucca hybrids of gardens appear for the most part if not always to be spontaneous or artificial crosses between the variegated and other forms cultivated under various names, but now generally referred to this species. Altogether *Y. aloifolia* is one of the species most worthy of study in its native habitat, since little is known except that it sometimes fruits without the aid of Pronuba, and that its seeds sometimes contain the larvæ of *P. yuccasella*, while the exact mode of pollination when the moth is excluded is not known from observation.

It is well known that *filamentosa*, when cultivated far north of its range, is uncertain in its blooming, although further south it flowers every year; and attention has been called frequently to the periodicity of *brevifolia* and other species in their native home.* No doubt this is connected with the previous conditions of nutrition, and the immediate climatic influences under which the plants have grown, but it appears quite remarkable that so many plants of *aloifolia* at the Garden, of very different size and age,

* Riley, *l. c.* 117.

should have bloomed together this year, after a long period of rest.*

The most striking morphological peculiarities of the species, aside from its rather stiff sword-shaped denticulate leaves, are the marked stipe of the ovary, and the decidedly hexagonal cross section of the ripening fruit, due to the rapid growth of the nectar grooves,— both of which features are well shown on plate 44 of the Third Report.

Y. YUCATANA, Engelm.— So far as I can learn, nothing is known of this species further than that it was collected in Yucatan by Schott, whose specimens are preserved in a few herbaria.

Y. GUATEMALENSIS, Baker (Pl. 1, 2, 19).—This species is said to occur in southern Mexico, as well as Guatemala. In August and September, 1892, a fine plant, said to have come originally from Haage and Schmidt as a Furcroea, bloomed in the Garden, synchronously with a form of *gloriosa*, but fully a month later than *aloifolia*. The pollination arrangements appear to be almost identical with those of *baccata*, which are described below. In this specimen the septal nectar glands, although they are not very large, were more active than those of any other true Yucca known to me, and their secretion appeared in rather copious drops at the base of the ovary, where the nectar grooves open, or in smaller drops near its top, where the glands open into the grooves, if, as frequently happens, the latter have spread somewhat. Artificial pollination gave a number of the very large pendent baccate fruits, but nothing is known of the natural pollinators of the species.

The fruit raised by artificial pollination is very stout. One of the larger (but not the largest) of the specimens measured $2 \times 3\frac{1}{2}$ in. and weighed, while still green, 6 oz. At first quite hexagonal in cross section, its intercarpellary facets ultimately disappear toward the base. The bases of the filaments are adherent to the base of the fruit, much

* Meehan (Monthly, ii. 190) mentions a plant which flowered for the first time when at least seventy-five years old.

as in *aloifolia*, and similarly reflexed. When fully grown, but not ripe, the fruit is of a clear apple-green color.

Y. SCHOTTII, Engelm. (*Y. macrocarpa*, Engelm.) (Pl. 3). — Though *Y. macrocarpa*, which appears to be only this species, is not uncommon in parts of southern Arizona, no observations have been made on its pollination, and I was unable to find it in bloom. Flowers collected in the Santa Rita Mountains, July 9, 1881, and in the Huachuca Mountains in September, 1882, show either an unusual duration of the flowering period, or great variability in it. *Y. elata* and *Y. baccata*, which are spring-blooming species of the same region, are pollinated by *Pronuba yuccasella*, which can scarcely be expected to occur as late as the dates mentioned; but *baccata*, in different localities, is known to have a prolonged period of blossoming comparable with that of the different forms of *filamentosa* in the southeast, so that it is possible that in its pollination arrangements *Schottii* bears the same relation to *baccata* that the autumnal *gloriosa* does to *filamentosa*.

Y. TRECULEANA, Carr. (Pl. 18). — This Texan and Mexican species is believed by Riley to be pollinated by a probably distinct Pronuba,* but no observations have been made on it. A specimen which bloomed in the Garden this season was quite as sterile as other cultivated Yuccas aside from *filamentosa* and *glauca*, which are pollinated by *P. yuccasella*, and the *aloifolia* noted above; and this has been the case on the several occasions when the specimen has bloomed in the past.

According to Engelmann† *Treculeana* is reported by Lindheimer as sterile in Texan gardens, though the wild plants are abundantly fertile.

Y. BACCATA, Torr. (Pl. 20).—With the possible exception of *Y. glauca*, this is the most widely distributed of our species, ranging in a variety of forms from southern Colorado into Mexico and to California, where it extends

* *l. c.* 122; Proc. Biol. Soc. Washn. vii. 96; Insect Life, iv. 371.

† Collected Writings, 284.

from about Monterey into the peninsula. It therefore connects the territory of *glauca*, which is pollinated by *Pronuba yuccasella*, with that of two Californian species pollinated by very distinct moths. No observations appear to have been made heretofore on its pollination, nor has any Pronuba been taken on its flowers, but Professor Riley predicts the probable discovery of a distinct species for it.*

In the valley between San Bernardino and Colton, California, *baccata* is found in some abundance, but no Pronuba was seen in any of the specimens examined about the middle of April, when they were in full bloom, and they are said never or very rarely to fruit there, by Mr. S. B. Parish, in whose company my observations on this occasion were made.

About Banning and Cabazon, on the western edge of the Colorado desert, where the plants are more abundant and of larger size, often with a trunk five or six feet high, they are more generally fertile, and a quantity of fruits of the preceding year were collected from the crowns of leaves into which they had fallen on maturity, and where they had been protected from rodents. Most of these fruits were strongly constricted about the middle, and perforated in places, where the larvæ of a Pronuba had escaped. The plants were not blooming very freely this year, but several specimens of a white Pronuba were taken resting in the flowers, and though numerous panicles had bloomed without setting any fruit, others were sparingly, and still others abundantly, fertilized, and the ovaries of the fertilized flowers showed unmistakable constrictions or indentations indicative of the oviposition of Pronuba; still, the moths were not sufficiently numerous to render night observations on their work possible.

A number of blooming plants of *baccata* were examined about the first of May on the mesas back of San Diego, where, notwithstanding the more southern latitude, the

* Proc. Biol. Soc. Washington, vii. 96.

season is later than on the desert and in the warmer valleys further north. On this occasion I was accompanied by Mr. C. R. Orcutt, who informs me that the seeds of *baccata* are in some seasons very much eaten by larvæ, probably of Pronuba;* and the cluster of perforated fruits figured on the accompanying plate was photographed many years ago in the same region. Though the oldest pistils were less developed here that at Cabazon, there was abundant evidence that they had been oviposited in by Pronuba, several individuals of which were taken in the flowers.

The flowers of this Yucca, though they are as variable in form as those of the eastern capsular species, agree, so far as I have observed, in having the sepals decidedly umbonate at the base, as is also frequently the case with *aloifolia*, so that each flower appears somewhat as if constricted immediately above the bottom. In color they range from creamy white, often with a tinge of green, to a decided brown purple, the perianth being always very glossy, and they are slightly and delicately fragrant. The minutely papillate filaments vary much in length, but commonly reach to about the base of the style, where they are more or less abruptly thickened and bent outwards. In one observed case, however, they were as long as the entire pistil. A curious feature observed in dried specimens as well as in recently fertilized flowers with drying stamens, is the strong recurving of the upper part of the filaments shown on plate 48 of the last Report, but never observed in fresh unfertilized flowers, as it often is in *Y. Treculeana*.

The anthers do not appear to dehisce quite as promptly as in the *filamentosa* group, where there is practically no dichogamy, so that in this species the Pronuba is more likely of necessity to have derived her load of pollen from another flower when she begins pollination on one which is newly expanded; but the protogyny noted scarcely extends beyond the evening on which the flower opens, so that it is

* Specimens of old fruit received since the above was written are badly infested by an undetermined beetle.

by no means as effective in preventing close fertilization as in *brevifolia* and *Whipplei*, which are described below. The bright golden yellow pollen is readily seen on any part of the flower in contact with which it may have come, and particularly, on the nearly white ovary and the pure white style.

The latter is not usually as long as in the flower figured in the last Report and already referred to. It has a very open stigmatic tube which passes into the upper ends of the ovarian cells, as may be seen in some cases even by looking down the wide channel with the aid of a hand lens, for there is little stigmatic secretion. In this species it is also very easy to convince oneself that the three pollen-conducting grooves, similar to those figured by Webber for *glauca** but also seen in Agave and other plants with this type of pistil, are formed by the uppermost part of the infolded edges of the carpels, which further down coalesce to form the true septa, and constitute the placentæ. As in other Yuccas, each septum of the ovary contains a nectar gland;† but the glands of *baccata* are not so large and open as in the *filamentosa* group of species, in this respect agreeing with those of the other fleshy-fruited Yuccas that I have examined. Notwithstanding this, they appear to be rather more active than in the former group (herein agreeing with *Guatemalensis* among the baccate species, *gloriosa* among the spongy-fruited species, and the Hesperoyuccas), their secretion sometimes appearing in small quantity at the base of the pistil, where their large ducts discharge. Several of the flowers examined at San Diego in the morning were very wet on the outside, a condition which has been observed on other species;‡ but though it is

* American Naturalist, 1892, 303, 309, pl. 13, f. 38.

† Trelease: Bulletin of the Torrey Bot. Club, 1886, 135, and Third Garden Report, pl. 53; Riley, *l. c.* 109, Proc. Biol. Soc. Washington, vii. 91, and Insect Life, iv. 364 to 366.

‡ *Y. filamentosa*,— Meehan, Proc. Phila. Acad. 1888, 276, and Trelease, Third Garden Report, 123; *Y. gloriosa*,— Meehan, Proc. Phila. Acad. 1880, 355, 1883, 191; and *Hesperoyucca*, mentioned below.

pretty clear that this fluid is not derived from the septal glands, its source is not evident.

A number of small beetles and flies visit the flowers, apparently attracted by the pollen, which in some cases they have been seen to eat. As was noted last year for *glauca*,* these insects sometimes dislodge masses of pollen from the anthers, and the length of the stamens in *baccata* may frequently cause some of this to fall upon the tips of the stigmatic lobes. In one case a small mass of pollen was found in this position, and, in another, some pollen had been pushed into the mouth of the stigmatic chamber, evidently having fallen upon the petals and been transferred to the stigma by the pressure of my hand as I gathered the flower. In some such way, therefore, perhaps exceptional pollination may be effected now and then in *baccata* when Pronuba is not present; but I should not expect this to be of frequent occurrence, and the observations at Colton show that it must be rare or ineffective.

The moths taken in the flowers of this species at Cabazon and San Diego are somewhat larger than many specimens of *Pronuba yuccasella*, and they appear to have the tip of the abdomen, the maxillary palpi, and the antennæ, as well as the chitinized parts in general when denuded, a little darker in color, but aside from these and the greater ease with which their scales are rubbed off, I can detect no characters by which they can satisfactorily be separated from *P. yuccasella* of the Mississippi Valley and Rocky Mountains, which is also said to be indistinguishable from the moth of the Gulf region.† Like the eastern representatives of *yuccasella* they rest within the flowers during the day, with their heads directed toward the base of the stamens, though they seem a little more ready to drop from the flowers when disturbed. Unfortunately I have been able to make no observations on their work, but the females bear loads of pollen of the usual form, and fertil-

* Cf. Riley, *l. c.* 125.

† Professor Riley has since confirmed this conclusion.

ized flowers show conclusively that they thrust this well into the stigmatic canal,— in some cases apparently even into the top of the ovarian cells, which, owing to the short style and the deep stigmatic notches, they can reach easily with their long maxillary tentacles. In ovipositing, they doubtless back down between the upper ends of the stamens, and the ovary is pierced at about its middle. The septa, and the median line of each cell (which is produced into the cell as a false dissepiment, dividing the cell into two), being covered by the appressed lower part of the filament, the moth is constrained to puncture the wall part way between the true and false partitions, as she commonly does in *filamentosa*,* this being also its thinnest part. At San Diego, where the moths were more abundant than at Banning, as many as three to five punctures in a vertical series were seen several times in one cell of an ovary, the other cells sometimes showing none at all.

The compound microscope reveals the presence of pollen in the stigmas of all such flowers punctured for oviposition as I have examined, and a hand lens commonly shows it, though not always. The open stylar canal is frequented by large numbers of a white Thrips, which sometimes penetrate into the cells of the ovary, and doubtless scatter the pollen greatly, perhaps devouring some of it. On dried fruits of the preceding season, the perforations made by escaping larvæ are commonly elevated, the uninjured tissue evidently shrinking more in drying than that immediately surrounding the tunnel of the larva. These dried fruits sometimes show constrictions corresponding to the points of oviposition, but they are frequently obliterated in the development of the pulpy exocarp.

Y. AUSTRALIS, (Engelm.). (Pl. 4, 5).—A study of material on the Sierra Blanca plateau of southwestern Texas, and a careful review of the literature of the species related to *baccata*, enables me to fix without further ques-

* Riley, *l. c.* pl. 36, f. 2.

tion the name *filifera* for the large Mexican "palma" with drooping panicle, for it has satisfied me that the greater part of Engelmann's *Yucca baccata*, var. *australis* consists of another form (from which perhaps one other species with erect panicle, in the upper Mexican plateau, may be separated ultimately). *Y. australis* is the large Yucca collected by Thurber about Parras, Coahuila, in November, 1852 (no. 1857, in Herb. Torrey.),* and said to become sometimes thirty feet high and two or three feet in diameter, by Bartlett,† who figures a much branched large specimen. It is also mentioned by Baker in the Gardeners' Chronicle for 1870, p. 1088, under the number 26, but without name; and by Engelmann (cf. Collected Writings, p. 292), as a variety under *baccata*. So far as I can judge from herbarium material, it was collected in Mexico by Coulter (no. 1571 in Hb. Gray.), and it appears to be the plant collected in the Carneros Pass, Coahuila, by Pringle in 1889 (no. 2841) and 1891 (no. 3912). It appears, therefore, to be a species of the northern high lands of Mexico, extending into the elevated Sierra Blanca region of Texas, where it is associated with other southern plants like *Agave applanata* and *A. Poselgerii*. Its nearest described allies, which Mr. Baker tells me have narrow leaves, are *Y. periculosa*, Baker, and *Y. circinata*, Baker, both of which, like the present species, have been referred usually to *baccata*, and which are yet imperfectly known.

Seedling plants have the blue-green leaves of *Treculeana*, and possess a cluster of rather fleshy fusiform roots becoming as thick as one's finger, but no central tap root. With age these roots are replaced by long, tough, cord-like roots as thick as a lead pencil. The trunks at length become a foot or two thick, and generally from ten to fifteen feet high, where my observations were made. Though

* Torrey, Bot. Mex. Bound. 221-2.

† Personal Narrative, ii. 490.

commonly unbranched or with only a double crown, they sometimes develop several large, more or less spreading branches. The very concave leaves are of a clear green color, and either entirely smooth to the touch or only slightly scabrous on the few angles which sometimes run longitudinally on the back. Their margin on unfolding is entire, purplish brown, and dilates into the firm but blunt brown tip, from which, after the leaves have expanded, it breaks away in the form of numerous stout gray or brownish fibers, pectinately spreading near the apex, and becoming longer and more remote below, so that ultimately the leaves are not filiferous except for a few crowded short fibers immediately below the point, and a more or less abundant aggregation of loose threads between their bases, causing a cobwebby appearance. The older leaves for a long time are reflexed against the trunk, and appear to be more fibrous and rigid than those of *Schottii* and *baccata*. The inflorescence is ample, recalling that of *Treculeana*, and the conspicuous white bracts sometimes measure as much as 3×12 inches.

In the Texan region indicated, this form grows with *Yucca elata*, *baccata* being absent; but it blooms a full month earlier than the associated species. Its fruit, like that of several of the other baccate species, is usually long beaked, and the seeds are tunneled in the manner characteristic of the work of Pronuba, the pulp being perforated by the escaped larvæ. I was unable to study this species in bloom, but large fruits gathered some three weeks after fertilization show none of the constrictions or indentations which so commonly mark the ovipositing punctures of the Pronuba moths, which leads to a suspicion that the eggs may be deposited in the upper part near the stigma.

Y. VALIDA, Brandegee. — In admitting this species to the list of Yuccas published in the Third Report, I had overlooked the fact that Mr. Brandegee* himself has referred

* Proc. Calif. Acad. (2), iii. 175.

it to *baccata*. The smooth leaves of the specimens I have seen are, however, quite unlike the rough foliage of the usual northern form of *baccata*, and the question of the distinctness of *valida* may still be kept open. I think it very probable that it will be found in the heart of Mexico, where several little-studied Yuccas of the *baccata* set occur, as well as in its present range on the peninsula of Lower California. Nothing is known of its pollination.

Y. FILIFERA, Chab. — Nothing is known of the pollination of this Mexican tree Yucca, except that herbarium specimens of its fruit show the work of Pronuba larvæ, from which Professor Riley infers that a large and interesting species of moth peculiar to it will be discovered.*

B. CLISTOYUCCA, *with leathery or spongy indehiscent fruits.*

Y. BREVIFOLIA, Engelm. (Pl. 6-9, 21)†.—This, our largest tree Yucca, is interesting from several points of view. Seedlings possess decidedly glaucous flexible leaves, rather similar to those of young *Whipplei*. At first a fleshy round-pointed caudex develops below ground, from which long simple tough roots spread in all directions; but this original descending axis disappears with age, so that the old tree has a flat or irregular basal disk, from which the tough roots, now as thick as a lead pencil, run into the soil for a long distance. As a rule each plant forms only a single trunk, but occasionally laterals develop, generally as a result of injury to the main stem. Until it is eight or ten feet high, the trunk is unbranched, and covered throughout with the very rough and rigid, mostly yellowish-green leaves, the lower of which are reflexed. When of about this size, it blooms for the first time (Pl. 6), after

* *l. c.* 121; Proc. Biol. Soc. Washn., vii. 96; Insect Life, iv. 371. As a further reference to this species should be given Fenzi: Boll. Soc. Tosc. ortic. xiv. 1889, 278, with plate.

† See an article by Shinn, on "The Land of the Tree Yuccas," in American Agriculturist, 1891, 689.

which two or three stout branches usually develop by the side of the original apex, which now has ended its growth. When these have reached a length of two or three feet each forms a terminal inflorescence, and branches in its turn, in this way giving rise to a repeated forking or tripartition. On an overturned trunk, however, several of the stronger branches usually become erect and grow to a height equal to that of young trees, before blooming and branching (Pl. 8), but so far as I have seen they do this without forming roots of their own, their supply of food and moisture coming through the persistent roots of the main trunk.* On the large stems, and even on some of the larger branches of old trees, the reflexed leaves gradually fall away, and expose to view a very thick gray bark, deeply fissured into quadrangles measuring about 1×2 inches. As the trunks increase in height they also become much thicker, the loosely fibrous, water-soaked wood being marked in concentric rings, resembling those of Dicotyledons and Conifers.† At the base, these older trees dilate quite abruptly, from the development of a circle of thick confluent roots, which correspond to those so commonly seen in the form of more or less marked prolongations of ridges and buttresses on Dicotyledons, and constitute the root-bearing disk mentioned above (Pl. 9). These large roots possess a structure superficially similar to that of the trunk.

When preparing to flower, this is one of the most attractive of all the Yuccas, the ovoid inflorescence buds, each as large as an ostrich egg, being closely invested by large thick white bracts, after the manner of a banana inflorescence; but the bracts soon become dry and crumbling, and the expanded cluster, though of very compact

* An excellent wood cut showing this habit of growth occurs in the Gray Herbarium, evidently clipped from one of the English horticultural journals, but I have been unable to obtain a more exact reference to it.

† The structure and mode of thickening in arborescent Liliaceæ is very fully treated by Röseler in Pringsheim's Jahrb. f. wiss. Bot. 1889, xx. 292–348, with several plates.

habit, is of an inconspicuous greenish white, and possesses an odor which is so oppressive as to render the flowers intolerable in a room, although the usual designation of fetid is not strictly accurate.* Though the flowers differ somewhat from the common Yucca form, they are quite as variable as those of other species of the genus, and range from globose to nearly oblong, or even prismatically pyriform when first opening. The petals differ from those of other species in being very thick, sometimes measuring as much as a quarter of an inch, and correspondingly rigid, and on different plants they vary from glabrous to very pubescent, and from glossy to quite dull, but usually with the waxen appearance so commonly seen in the genus.

The filaments here are generally much shorter than the pistil, against which they are very closely applied except near the top, where they are often clavately thickened, and the lower part is usually villous papillate. The pale lemon yellow anthers differ strikingly from those of eastern species, and in degree from those of other Californian Yuccas, in dehiscing only some forty-eight hours after the flower has opened, while the stigma appears to be fully receptive at the time of first expansion.

The whitish-green almost conical pistil is destitute of a clearly marked style such as *baccata* and *filamentosa* show, but its upper part is not occupied by the ovarian cells, and so is virtually stylar. The lobing between the carpels at top is so slight that the stigma is almost equally 6-notched. The stylar canal is rather ample above, but its connection with the ovarian chambers is through a series of slits, rather than open pores, and, at least after pollination, the passages are often occluded by the conducting tissue. The septal nectar glands are less developed in this species than in any other which I have studied. They are always narrow, and in some cases do not reach below the upper third

* *Cf.* Parry, Amer. Naturalist, i. 141; abst. in Gardeners' Chronicle, n. s. iii. 492.

of the ovary. Externally they open in the usual manner, but the deep outer septal grooves are little if at all expanded into a conducting channel, though they reach to the base of the pistil in the usual manner and expand there into triangular spaces. I have not observed any evidence that the septal glands secrete at all, nor is the stigmatic secretion as abundant here as in most species.

The dark colored *Pronuba synthetica*, which Professor Riley * describes as peculiar to this Yucca, rests during the day within the flowers in much the position already described for the eastern *P. yuccasella*, or, especially when disturbed, retires between the densely crowded flowers, where it is protected from most dangers; but it is more active through the day than its eastern congener. Towards evening the moths become quite active, and it is probable that copulation of the sexes occurs before night, for I have not seen male moths at night within the flowers where the females were occupied in oviposition. There is also reason to believe that the latter accumulate their loads of pollen at an early hour, though this again is only inference, since I have not witnessed the operation, even in the cases in which I have suspected that a moth was so employed, owing to the peculiarly closed condition of the flowers. Unlike the other known species, this Pronuba appears slow to take flight. Though it is easily disturbed, so as to run about and seek concealment between the flowers, I have seen it take to the wing only a few times, and then it merely sailed down to the ground, not far from the tree. This apparent indisposition to leave the flowers may, perhaps, be connected with the almost constant occurrence of high winds on the desert. Whatever its cause, this habit of the moths appears to restrict cross-pollination to flowers of the same plant more closely than is the case with other Yuccas, though there must be frequent flights from plant to plant

* *l. c.* 121, 141; Proc. Biol. Soc. Washington, vii. 94; Insect Life, iv. 370. (This was first called *P. paradoxa*, but without description.— Riley Proc. Wash. Ent. Soc. 1888, i. 154, and Insect Life, i. 372.

in quiet weather, and especially at night, when the wind sometimes falls; and the development of the stigma two days in advance of the stamens of a given flower, renders close fertilization in the strictest sense improbable.

The light yellow pollen is in such marked contrast with the smoky tint of the moth, that laden females are recognizable from a considerable distance, and notwithstanding the failure of direct observation, there is every reason to believe that the latter collect their burden from the older flowers with the same deliberateness that has been observed in the other known species of Pronuba, since it is held under the well developed tentacles in the same manner as by them.

On first examining the flower clusters of *brevifolia*, I was impressed by the remarkable symmetry of most of the fertilized pistils, some of which had already reached half the size of the mature fruit, which is in marked contrast with the constriction or indentation of the eastern capsular Yuccas at the point where the ovary has been punctured in oviposition. This absence of deformity was explained, however, when the act of oviposition was witnessed, for the moth pierces, in this species, the uppermost part of the style, conveying its eggs down to the ovary through the stylar channel,— the course followed by the pollen tubes.

The female of most species of Pronuba seeks for a fresh flower in which to deposit her eggs, showing preference for one in the first night of expansion. To this she is probably impelled by the impulse to insure for her offspring a sufficient supply of food, the younger flowers being less likely than the older to be already overstocked with eggs. This instinct is particularly marked in *P. synthetica*, which I have never seen ovipositing in any but the youngest flowers, while I have repeatedly seen the pollen-laden moths force themselves into the very narrow clefts between the rigid sepals of an opening bud, their flattened form facilitating this, after which only the most fragmentary glimpses of their work were possible. But during something over a

week in the early part of April, spent at Hesperia, California, where *brevifolia* is very abundant, I was fortunate enough to observe many of the moths at work in somewhat more open flowers, where their operations could be observed in detail by the use of a bull's-eye lantern, to which they show about the same tolerance as the other species.

When about to deposit an egg, having selected a suitable flower, the female of *synthetica* runs to the bottom of the stamens much as *yuccasella* does, makes a rapid more or less complete circuit of their bases, and then quickly ascends to the very top of the pistil, her thorax rather higher than the end of the stigma, and with her short but strong ovipositor cuts through the thin wall, into the stylar channel, rarely as much as 2 mm. below the tip of the stigma, meantime holding fast to the pistil, the stamens being below her reach. The long extensile oviduct is then passed through the puncture, the egg being laid apparently within the ovarian cell, along the funicular end of the ovules. In removing the oviduct the moth not infrequently carries her body across the stigma, so that at first sight she appears to be withdrawing it directly from the mouth of the stylar canal; but I have never seen her make direct use of this canal. The operation consumes more time than does the oviposition of either *yuccasella* or *maculata* as I have observed them, and usually takes altogether from two-and-a-half to three minutes. Sometimes two or more eggs are laid before the stigma is pollinated, but commonly after laying each egg the moth retreats to the bottom of the flower and then again ascends the pistil until her head is brought even with the stigma, when she uncoils the large tentacles from their resting-place against her load of pollen and passes them back and forth in the stigmatic chamber, with almost the same motion as the eastern species, usually making use of one of the stigmatic notches. While so employed she carries the rather short tongue almost straight out above the stigma, but I have never seen her make any use of it to force pollen into the latter, nor has she been

observed to attempt to feed on the slight stigmatic secretion nor to search for food at the base of the flower, where, if anywhere, the nectar of the septal glands should be found.

In this Yucca, the short spreading pedicels do not become erect after the fertilization of the flowers, as is the case in the capsular species, nor do they become markedly pendent as in *gloriosa* and all of the baccate species, but they maintain their original direction during the ripening of the fruit. As in all of the Yuccas, the maturing fruit develops a rather firm but thin core-like endocarp immediately surrounding the seeds, but in this species the thick exocarp, instead of becoming pulpy as in the baccate species, or hard as in the dehiscent capsular section, assumes a spongy texture. The ripe fruit, readily breaking from the tree, consequently possesses large bulk and low specific gravity.

Y. GLORIOSA, L. — Professor Riley* states that this species, which occurs in the *aloifolia* region of the southeast, is pollinated by *Pronuba yuccasella* when it chances to bloom in the season of the moth, which appears when the earlier forms of *Y. filamentosa* are in flower; but its blooming is more commonly later, often autumnal, so that it less frequently produces fruit than *aloifolia*, and Dr. Mellichamp writes me that although he has seen many blooming plants he never has seen fruit of *gloriosa* but once, and that was from a summer inflorescence. Like *aloifolia*, the present species, in some of its rather numerous forms, is said to fruit occasionally when Pronuba does not occur to pollinate it.† Engelmann has shown, how-

* *l. c.* 116, 117.

† Ellacombe, in the Gardeners' Chronicle for 1880, xiii. p. 21, reports that in England he has more than once had well formed fruit on *Y. recurvifolia*, but the seeds did not come to maturity; and in the same journal for 1885, xxiv. p. 628, he mentions what appears to be the same form, under the name of *Y. recurva*, as having fruited in 1876, some of the fruits and seeds having been sent to Kew and to Dr. Engelmann, a few abortive fruits, which soon fell off, having also appeared in 1885. On

ever, that forms of *aloifolia* have been cultivated frequently under the name of *gloriosa* or wrongly referred to that species,* and an editorial mention in the American Agriculturist for 1872, xxxi. p. 461, of the apparent absence of insects from the pulpy fruits "as soft as a banana" of *gloriosa*, in Georgia, undoubtedly refers to *aloifolia*. Professor Riley limits the power of self-fertilization so far as known to *aloifolia*;† and it may be questioned whether the French *gloriosa* seedlings mentioned by him in a quotation from The Garden‡ were not really *aloifolia*, though it is not distinctly stated that they were not the result of artificial pollination. I have no personal knowledge of the fruiting of true *gloriosa* except in the case figured on plate 7 of the Third Garden Report, where a specimen cultivated in Washington produced fruit side by side with a plant of *aloifolia*, and in this case the fruits were more or less deformed, as if by Pronuba.

A rather narrow-leaved form of this species, cultivated in the Garden under the name of *Y. nivea*, bloomed in the early part of September, 1892, and showed nearly as great activity of the septal glands as the specimen of *Guatemalensis* already described, the nectar appearing in considerable drops within the bottom of the perianth, about the almost pilose bases of the filaments. While the *aloifolia* of the Garden was fruitful without the aid of Pronuba or hand pollination, and both *aloifolia* and *Guatemalensis* yielded fruit when artificially pollinated, this plant set no fruit, though a number of flowers were pollinated by Mr. Webber. It will be of interest, therefore, to have observations made on *gloriosa*, whether wild or cultivated in its native region. The later blooming of this species,

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the other hand in a popular account of Yucca pollination, in his Pflanzenleben, ii. 155, Kerner von Marilaun states that the fruit of this species is quite unknown both on wild and cultivated plants, and it is said that the moth adapted to *gloriosa* has become extinct.

* Trans. St. Louis Academy, iii. 211; Collected Writings, 297–8.

† Proc. Amer. Assoc. Adv. Sci. xxxi. 467.

‡ Proc. Amer. Ass. Adv. Sci. xxix. 624.

like that of certain forms of *filamentosa*, involving, as it appears to do, a loss of the services of Pronuba and consequent sterility in all but exceptional cases of early blooming, is especially worthy of study, considering the usual close correspondence of the period of blooming of the Yuccas with that of the appearance in the perfect form of their Pronubas.

C. CHÆNOYUCCA, *with dry, septicidally dehiscent capsules.*

Y. RUPICOLA, Scheele. — No observations have been recorded on the pollination of this Texan species, which Professor Riley* believes may have a distinct Pronuba. It is not uncommon from Fort Worth southward, on the black soil with intermingled limestone, but I failed to study wild plants. At Dallas, however, through the kindness of Mr. J. Reverchon, I was able to examine specimens cultivated on his place, which were blooming simultaneously with the wild *Y. glauca*, var. *stricta* and frequented by *Pronuba yuccasella* like the latter. These plants are abundantly fertile (each crown dying after blooming), and the structure of the flower indicates that the moth works on them as she does on the *filamentosa* group, though I was unable to observe her actions. Their seedlings are now spontaneous about the place, and so variable that Mr. Reverchon suspects hybridization with the native variety of *glauca*, as well as cultivated forms of *filamentosa*. This will prove an interesting subject for future study, since the habits of Pronuba in caring for her young are so highly specialized, and the details are so minutely carried out, that it was hardly to be expected that a given individual would indiscriminately pass from one species of Yucca to another, though on the other hand, it is known that the more eastern species are all pollinated by representatives of the single species of Pronuba.

Y. ELATA, Engelm. (Pl. 10, 15, 22).— Beginning in western Texas, about the limits of *glauca*, this Yucca gradually

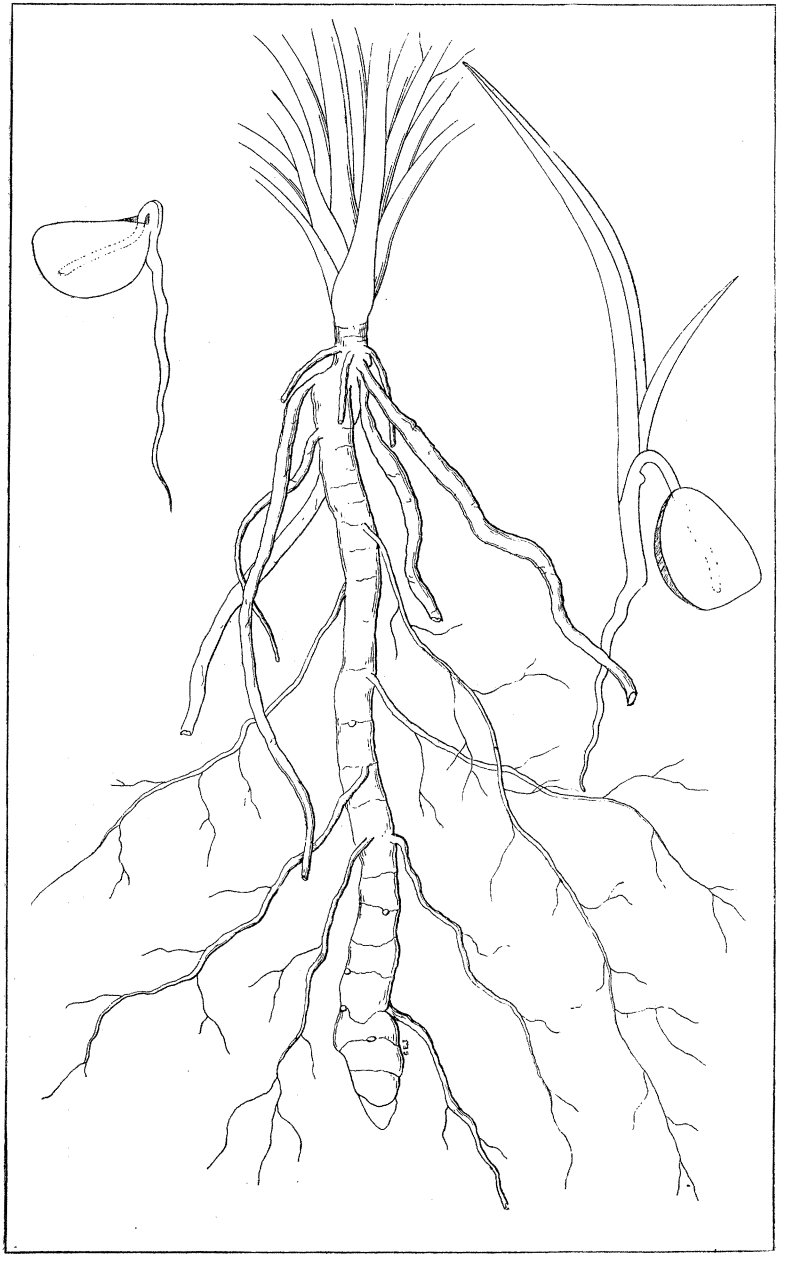
* *l. c.* 122.

increases in size as one passes into Arizona, where it becomes a rather large tree, but of far simpler habit than *brevifolia*, and much smaller than the larger plants of that species. Its underground axis is of the *glauca* type, — long, tough and branched,*— so that it is difficult to remove even the very small plants from the ground. The inflorescence appears to be terminal, so that the crown which has bloomed has its apical growth destroyed; but a lateral bud develops into a new crown, and in time a number of thick new heads may form in this manner, making a pluricapitate plant. The shortness of these branches, and their dense covering of long spreading leaves, contrasted with the frequent slendernesss of the trunk, after its lower leaves have become reflexed and dry, gives the tree a peculiar and not ungraceful appearance, quite different from that of any other species native of the United States. The old flower stalks, when above the reach of cattle, usually hold their dehiscent capsules for at least a year, and at length break away without disarticulation above the base, which persists for years along the side of the stem, closely applied to it because of the erect sympodial habit of the latter.

At Eagle Flat, Texas, I was able to spend several evenings about the first of June in studying the pollination of this species, which there rarely becomes six feet high and begins to bloom when not more than two feet high, so that observations are more readily made than on the taller plants of southern Arizona.

The flowers are nearly pure white, with quite acute thin petals, and conform in most respects to those of *glauca*. The style, however, is white, as in *rupicola* and *filamentosa*, and its segments are little thickened dorsally. The septal nectar glands are very well developed, as in all of this group, and reach to the base of the ovary. They appear to be slightly more active than in related species, for a little nectar was recognized in several flowers, and two

* Engelmann, Coll. Writings, 279, 280.



YUCCA ELATA AND FILAMENTOSA.

species of small bees* were taken, probing the outlets of the conducting grooves at the base of the pistil; but these insects were not seen to visit the stigma, so that they play no part in pollination. Considerable numbers of a moth, which Professor Riley determines for me as *Acontia Arizonæ*, Hy. Edw., were seen resting in the flowers during the day, and settled about them, especially on the pedicels near the base of the perianth, at night, but I was not fortunate enough to determine the occasion of their visits to the plant, though I suspected that their larvæ might develop on it. So far as can be seen, they play absolutely no part in its pollination, though it may be that they feed to a greater or less extent on the nectar. The stamens shed their pollen promptly on the opening of the flowers, and this is devoured by various small flies with the same avidity as in *glauca*, and with about the same prospect of effecting occasional casual pollination as in that species.†

Like the eastern Yuccas, *elata* is pollinated by *Pronuba yuccasella*, the work of which was repeatedly observed in detail at Eagle Flat, where the moths were abundant. During the day, like the Eastern moths and those of *baccata*, they rest in the flowers with their heads directed to the base of the petals. Shortly before sunset many of them become active (as is the case on *filamentosa* at St. Louis), the females beginning their work of oviposition and pollination, while the males run and fly actively from flower to flower in search of their mates; and this is continued through the greater part of the night.

When about to deposit an egg, the moth here, as on *filamentosa*, runs nervously about within the bottom of the flower, then scrambles to the top of the pistil and backs down between two stamens by a succession of jerks until her head is about level with the base of the style. Holding to the pistil by the pro- and meso-thoracic legs, the last

* Determined by Mr. Charles Robertson as *Agapostemon Texanus*, ♂, and *Halictus albipennis*, ♀.

† See a note by the writer in Riley, *l. c.* 125.

pair not infrequently carried out over the filaments, she then punctures the ovary and the egg is consigned to its place in the manner so well described by Riley for *filamentosa;* but as a rule the operation appears to consume rather less time on *elata* than on the other Yuccas I have studied. Usually each oviposition is followed by pollination, in which, so far as I can see, the moth acts precisely as on *filamentosa;* but in a few cases two eggs were laid before pollen was carried to the stigma, and under the bright light of the lantern the actions of the moth are sometimes so disturbed that she will leave a flower after ovipositing, without subsequently pollinating it. I have also observed on this species that she sometimes interrupts the act of pollination to coil the tentacles against her load of pollen, after which they are again inserted in the stigma, thus securing for the latter a larger amount of pollen; but I have no doubt this procedure is as common on the other species pollinated by *yuccasella.* In one instance, a moth disturbed by the light while ovipositing left the flower without pollinating it, but her first act on going into another flower was to thrust her pollen-laden tentacles into the stigma, though it appears to be unusual for this to precede oviposition.

The collection of pollen from the anthers was not closely observed on *elata*, but on several occasions the moth, when disturbed in oviposition, ran upon a stamen, shaking it quite violently and making several passes at the anther with her tentacles, as if impelled by fright to discontinue one of her customary occupations only to engage in another,—though her motions were too quick and nervous for me to see that she actually gathered any pollen. There is, however, no reason to doubt that the collection of pollen is similar to that on *filamentosa*, where, however, it is by no means always slow and easy of detailed observation.

When I passed over the Texas and Pacific road again, about a month later, a fair crop of partly grown fruits was seen, the usual constriction or indentation being noticeable over the Pronuba punctures. At Benson, in southern

Arizona, where *elata* assumes much larger proportions, though it bloomed very freely this year, I did not succeed in finding any of the moths in a day-light search in the early part of June, just as the species was coming into bloom, nor were many ripening capsules to be found when I again visited this locality toward the end of the month. But the few fruits which had set showed the usual Pronuba deformity, and a considerable number of last year's capsules were found, all containing the remains of tunneled seeds, and perforated by the escaped larvæ.

Y. GLAUCA, Fraser, Cat. 1813, not Sims. (*Y. angustifolia*, Pursh, 1814, and most recent writers).*— It has long been known that the pollinator of this representative Rocky Mountain species is *Pronuba yuccasella*, which appears coetaneously with its flowers in the west and southwest, but, being more closely connected in the east with the later-blooming *filamentosa*, only exceptionally appears early enough to pollinate even the latest blooming flowers of *glauca* on plants cultivated in Washington and St. Louis † (where a few capsules were again matured in the summer of 1891). The only observations on the behavior of the moth on wild plants that I know of are those reported by the writer in 1891 from the vicinity of Manitou, Col.‡ Incomplete as these are, they show that her actions are quite the same as on *filamentosa*.§

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* Though for reasons of expediency it would be better to preserve for this plant the name of *angustifolia*, under which it is universally known, the short description in Fraser's Catalogue is sufficiently characteristic, in connection with the northern locality from which his specimens were obtained, to make it necessary to restore his name. The later *Y. glauca*, Sims, is an entire-leaved plant which I should refer to *filamentosa*.

† Riley, *l. c.* 116, 121, 128. ‡ See Riley, *l. c.* 124.

§ The principal references under this species are as follows: Bruner, Entomol. Bull. U. S. Dept. Agriculture, ii. 9. Meehan, Bull. Torrey Bot. Club, iv. 63; Proc. Phila. Acad. 1873, 414; Proc. Amer. Ass. Adv. Sci. xxx. 205; Amer. Nat. 1881, 807; Proc. Phila. Acad. 1888, 275, general abstracts in Proc. Amer. Ass. xxxvii. 284 and Bot. Gaz. 1888, 237. Riley, Trans. St. Louis Acad. iii. 570; Mo. Ent. Rept. v. 159; Insect Life, i. 368; Rept. Mo. Bot. Gard. iii. various places.

The typical *Yucca glauca*, as represented in Colorado and Kansas, spreads below ground by a series of rather slender but very strong axes, and in its more highly developed form has a more or less developed mostly prostrate stoutish trunk above ground. So far as I know, whether caulescent or acaulescent, a given axis usually blooms repeatedly.

Y. GLAUCA, var. STRICTA, (Sims.). (*Y. angustifolia*, var. *mollis*, Engelm.) (Pl. 22).— In its broader flaccid leaves, occasionally an inch wide, this forms an approach from *glauca* to the Eastern *filamentosa*, but its range, — Arkansas, Louisiana and Texas,— brings it strictly within the region of the former and its immediate allies. Unlike the more representative *glauca*, however, a given crown seems more likely to fruit but once, though the subterranean parts are similar in both. Its delicate greenish-white flowers, most commonly in a simple raceme, possess the general characters of those of the type, and are slightly fragrant. The styles, though somewhat variable in color, are commonly bright green as in the type, so that they contrast with the ovary, which is colored similarly to the perianth. The stylar canal is open and in evident communication with the cells of the ovary, and at times contains a plentiful secretion. No nectar was observed at Dallas, Texas, where I had an opportunity of examining the flowers in several localities, but the septal glands are large and with large conducting grooves, as is generally the case in the *filamentosa* group.

Many years ago Boll * made a number of observations about Dallas on the Yuccas, some of which were doubtless of this variety. While he did not at first discriminate between Pronuba and the related *Prodoxus decipiens*, — which Professor Riley has well called the Bogus Yucca Moth, — and especially the still more deceiving *Prodoxus intermedius*,

* Boll, Stettin. Entomolog. Zeitung, 1876, 401, quoted by Riley in Trans. St. Louis Academy, iii. 571.

and fell into some other serious errors, he appears to have been the first to observe the collection of pollen by the female Pronuba, though not with the detail given by Professor Riley in the account of his own observation of this operation on Y. *filamentosa*.*

The pollinator of this variety, as of the more representative form of the species, is the white *Pronuba yuccasella*. As on other Yuccas, the moth is quite sluggish within the flowers during the day, apparently considering itself concealed by its protective coloration. Numerous laden females were taken and observed about the flowers at night, and copulation within the flower was several times seen in the evening, but I was unfortunately not able to see these moths engaged in either pollination or oviposition. The pale pollen, however, is very evident in the green stigmas, where there is little reason to doubt they have placed it. Egg punctures were also observed in numbers, in such a situation on the ovary as to show that the moth occupies the same position when ovipositing as on *filamentosa*. On the older panicles a fair percentage of fruit was maturing at the time of my examination at Dallas, and showed the usual Pronuba constrictions, and several capsules of the preceding year which were found had been perforated by escaping larvæ, and contained remnants of tunneled seeds.

At Putnam, Texas, considerably west of Dallas, a larger form of what I take to be this variety of *glauca* occurs, with narrower leaves; and about the end of May this was passing out of bloom, just as *elata*, still further west, was beginning to flower. At this place, fewer capsules had set than about Dallas, but these showed the irregularities indicative of oviposition by Pronuba, which had quite disappeared; and some of the stalks of the preceding year still bore capsules which were marked by the escape perforations of her larvæ.

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* Proc. Amer. Assoc. Adv. Science, 1882, xxxi. 467–8; Third Garden Report, 106, pl. 38, f. 2.

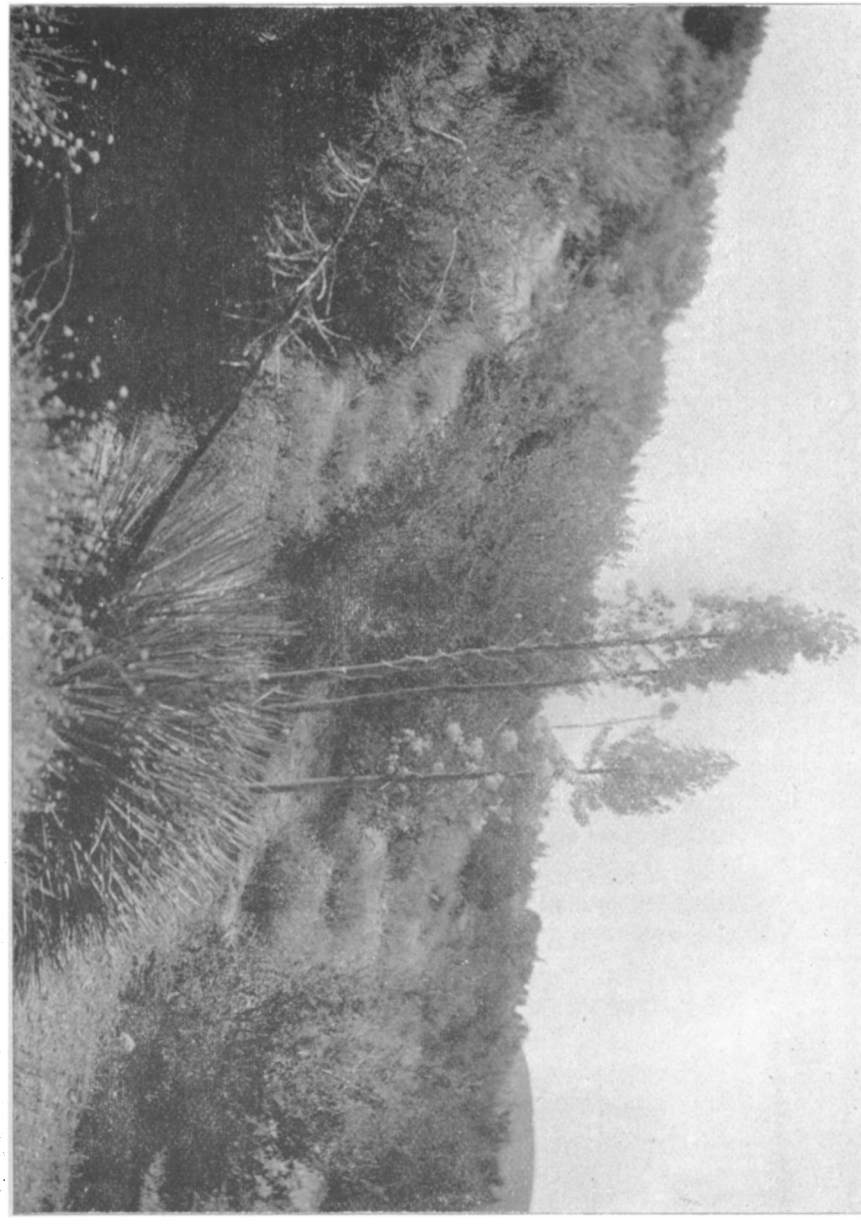
Y. FILAMENTOSA, L. (Pl. 11, 22). — This species is the subject of nearly all of the pollination observations heretofore published, and its interrelations with *Pronuba yuccasella* are so well known that I need scarcely do more than refer to Professor Riley's account in the last Garden Report. In St. Louis the observations of preceding years * have been repeated by myself and others, and on several occasions the collection of pollen was again witnessed, but in the same imperfect manner as last year, owing to the haste of the moth. Although special attention has been given to this point I have failed to see the moth attempt to feed on either the stigmatic secretion or the septal nectar, nor have I been able to reconvince myself that she makes use of the tongue in pollination, as I once thought. As in the case of *Yucca elata*, the moth, when disturbed by the lantern while ovipositing, sometimes attacks the stamens, as if intending to reinforce her load of pollen, but in most cases without proceeding far in this before retreating to the resting position within the base of the flower, or leaving the latter. In addition to the insects heretofore seen in the flowers of this species, I have this year seen several specimens of a rather large flower beetle, *Trichius piger*, in the bottom of the flowers, with their heads at the outlet of the nectar grooves as if feeding on the small amount of secretion.

HESPEROYUCCA.

Filaments adnate to the petals below: pollen agglutinated in coherent masses: style slender: stigma capitate, hyaline-papillate, with a microscopic axile canal: fruit capsular, loculicidal.

Y. WHIPPLEI, (Torr.) Baker. (Pl. 16, 23).— From the San Bernardino Mountains north to the latitude of Monterey and south into Lower California in the Coast Range, this peculiar species is very abundant, especially

* See Riley, *l. c.* 123 etc. Ellacombe in the Gardeners' Chronicle for 1872, p. 1457, Morse, *ibid.* 1885, xxiv. 598, and Smith, *ibid.* 1872, 1391, report spontaneous capsules on this species in England. This should be compared with the references given under *gloriosa*.



HESPEROYUCCA WHIPPLEI.

through the Tehachapi region, the lower mountains being often densely covered with its large frequently cylindrical panicles or old fruit stalks. The most typical form, as it occurs in the Cajon, Tehachapi, and San Luis Obispo regions, is almost always cespitose, sometimes with eight or ten crowns clustered over a single root, owing to the formation of lateral branches near the base of the main stem, even while this is quite young. After blooming, a given crown dies, but the several heads of these cespitose plants may prolong the life of the plant through a series of years, until the last of them has flowered. The leaves of this form are commonly, though not always, quite rigid.

The flowers are as variable as in the true Yuccas, ranging from globose to bell-shaped, and there are great individual differences in the degree to which they expand, but they are not typically rotate, as Dr. Engelmann was led to believe by some photographs looking directly into rather widely opened flowers. They differ from those of other species in having the glabrous (but still minutely granulated) filaments attached to the lower part of the petals,—a character not well shown in the figures in the last Report, so that as they open the stamens are drawn away from the ovary instead of lying in close apposition to it. The small oval anther cells are commonly tipped by a bunch of white hairs, though in specimens observed on the mountain sides above San Luis Obispo these were reduced to one or two on each cell or were apparently entirely wanting, and I have no idea as to their function. On dehiscing, the cells contract in such a manner as to expose the pollen freely, but at the same time prevent it in most instances from falling out, as it so frequently does in the true Yuccas. As Riley has already shown,* the pollen of this plant is not loose and powdery, as in Yucca proper, but glutinous. The contents of each anther cell, in fact, form a rather consistent two-lobed moist mass, which is held by its lower part but protrudes prominently from the open anther.

* *l. c.* 126, 139.

The pistil differs materially from that of the true Yuccas in having the ovary free from those longitudinal depressions which usually correspond with the appressed stamens, and in possessing a short contracted style surmounted by a capitate stigma, green toward the center, where it appears slightly indented, and covered with very long hyaline delicate papillæ which are always moist with abundant secretion that at length becomes almost gelatinous over the middle of the stigma. From the central depression of the stigma, a fine but unobstructed canal passes down the style and communicates with the top of the cells of the ovary. The nectar apparatus is well developed, the septal glands, though narrow, commonly reaching to the base of the ovary, while the conducting groove is of corresponding size. My observations lead to the conclusion that the glands, though smaller than in the *filamentosa* group, are more active than in other species studied by me, with the possible exception of *gloriosa* and *Guatemalensis*, for I have repeatedly seen considerable drops of nectar at the basal outlets of the grooves, especially in the early morning or in damp foggy weather when evaporation was slow, and in pendent flowers similar drops have been seen several times over the grooves at either the middle or top of the ovary, along the smooth surface of which they had apparently rolled from the outlets of the conducting grooves.

Professor Riley has shown that *Whipplei* is pollinated by a distinct Pronuba, which he names *P. maculata*, of a white general color, but somewhat variously mottled with black, especially towards the ends of the wings.* He records the occurrence of the moth in the vicinity of San Diego, Los Angeles, Newhall, and Caliente. I have also taken specimens at Summit in the Cajon Pass, at Saugus, San Luis Obispo, and along the Santa Ynez river above Santa Barbara, besides seeing evidence of its work in the

* *l. c.* 121, 139; Insect Life, iv. 370, note. For other notes by the same author, see Proc. Ent. Soc. Washington, 1888, i. 154, and Insect Life, i. 372.

old fruits both at Newhall and Caliente. The only other insects observed by me in the flowers, were small flies and beetles similar to those so frequently seen in the flowers of the Yuccas, a few small bees, and on one occasion, hive bees. The latter were primarily attracted by an abundant watery fluid on the outside of the flowers, of undiscovered origin,* and entered the flowers only incidentally. The others gathered nectar from the base of the corolla, where the nectar grooves open. Neither were seen to touch either the anthers or stigma, and it is doubtful if they carry pollen from one to the other, even by accident, which is the only way in which this could happen.

From its pronounced fragrance, which while it is of the general yucca type somewhat recalls that of the tuberose, its active nectar glands, pollen aggregated into crude pollinia, and large capitate stigma covered with long moist papillæ, *Whipplei* would appear quite likely to be pollinated by visitors other than Pronuba; and, as Professor Riley has well said, of all the Yuccas it would seem to be most easily self-fertilizable. In fact, in the lower part of the Cajon Pass when the species was in the best of its blooming period, very few Pronubas were seen; and, while there was a corresponding scarcity of setting fruit, a few plants were found with more or less abundant, partly developed but unusually diminutive capsules in which no oviposition scars could be detected, and some of the fruit of the preceding year was of the same dwarf character and without either escape holes or the masses of tunneled seeds almost invariably seen in old capsules elsewhere. Frequent observation has shown that the pollinia may be deposited on the margin of the stigma directly from the anthers in closing flowers, particularly the small ones to which these dwarf capsules correspond; and it was, therefore, with no little surprise that I noted, in contrast with this apparent power of self-fertilization, that with this single exception, no

* See note under *baccata* for the occurrence of a similar exudation in species of Yucca proper.

fruit whatever was found except that which clearly showed the work of Pronuba. At best, therefore, I should say that where its proper Pronuba is absent, *Whipplei* has only the limited power of self-pollination, or pollination by other agents, that is possessed by *aloifolia* among the true Yuccas. I have also no evidence that pollen tubes ever develop in such a manner as to reach and fertilize the ovules from pollinia placed on the margin of the stigma, although search was made for something of the sort; and a determination of the extent to which fertilization in this manner is possible must be made by a series of experiments such as I could not carry out in the time at my disposal.*

The characters of *Pronuba maculata* have been so fully given by Riley that nothing need be added to his description. From the frequently open character of the flowers, and, especially, the withdrawal of the stamens from the pistil, these moths are, however, constrained to behave quite differently from the other species of their genus; and very probably in connection with the more diurnal nature of the Hesperoyucca flowers, they are far more active in the day time than their congeners are. Unless locally absent, they are readily observed whenever the flowers are examined, either resting in them or engaged in pollination or oviposition, and at first sight it is difficult to say whether they are quiescent or engaged in the latter operation, for, unlike the other known Pronubas, they rest with the head toward the stigma, usually standing upon the side of the ovary, — a position almost identical with that taken in ovi-

* Since the above was written, Professor Riley, under date of October 13, 1892, writes me that in a manuscript report on the pollination of *Whipplei*, Mr. Coquillet of Los Angeles records the seeding this year of a number of pods or panicles which he had covered with gauze before any of the flowers opened. Professor Kerner von Marilaun (Pflanzenleben, ii. 155, figures 1 to 5), states that in repeated cases of blooming in the Vienna Garden this species has never matured its fruit. The figures which accompany his account of Yucca pollination represent some Euyucca, — apparently a form of *filamentosa*, — though they bear the name *Whipplei*; and the moth represented as pollinating the flower (adapted by the artist from Riley's figures), is *yuccasella*.

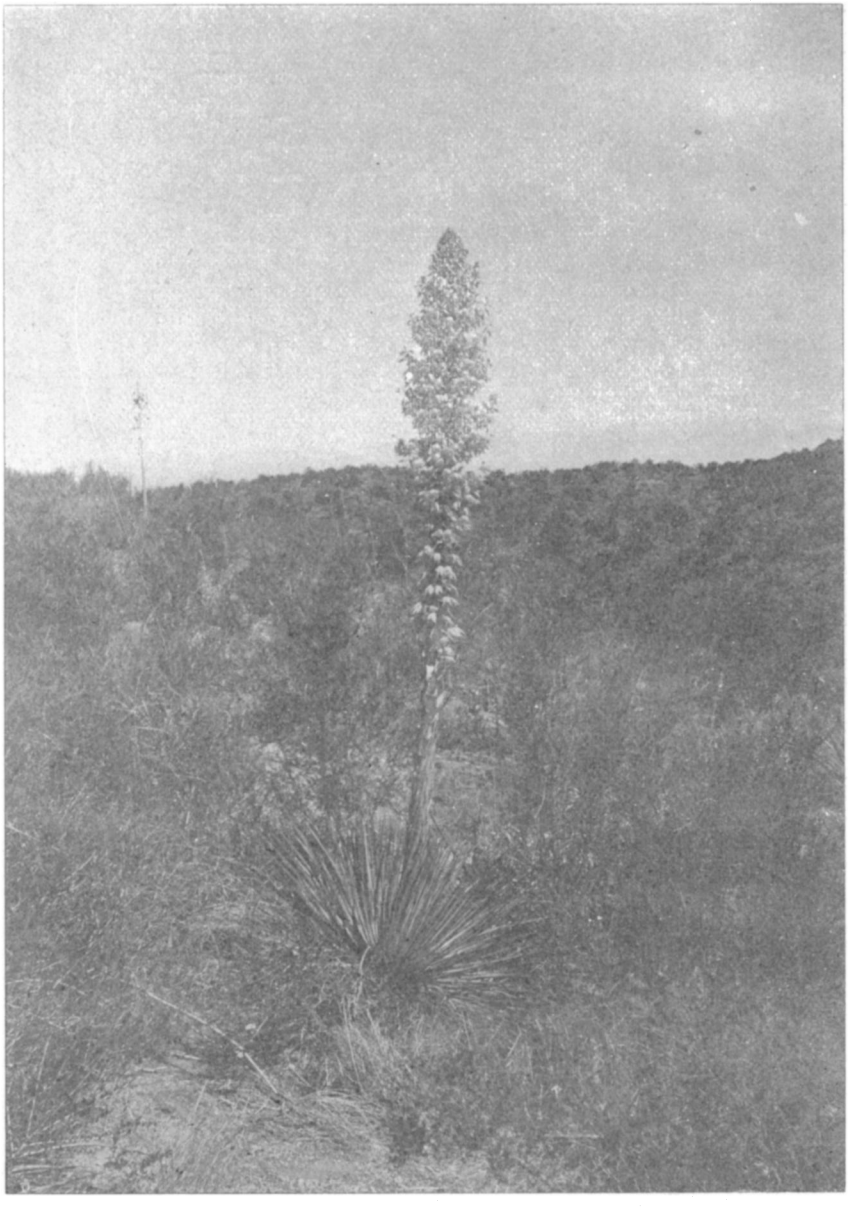
positing. While in this attitude they are very observant, and the approach of one's face, even at a distance, causes them to retire further down the pistil. When so disturbed they are also very apt to drop suddenly from the flower and take wing, seeking a new retreat.

I have not seen the collection of pollen by the typical form of this moth, but, from the way in which the load is carried, there is no doubt that it is accumulated in the manner presently to be described for the pollinator of what I take to be the *Yucca graminifolia* of Wood, and I see no reason to doubt that it frequently takes place in the bright daylight, as both oviposition and pollination do. Either of the latter operations may be witnessed at any time during the day, if the flowers are not approached too suddenly.

When the moth is about to deposit an egg, she usually moves about in the lower part of the flower much as the other species do, commonly dragging the tip of the ovipositor along the parts she walks on as if wiping off extruded secretion, but also seemingly using it as a tactile organ while she assumes the position best suited to oviposition, which is nearly the same as that taken while at rest. Standing on the side of the pistil, she then bends the abdomen sharply forward so as to bring the ovipositor to about the middle of the ovary, which she pierces at the thinnest part, namely, about 1 mm. from the septal groove. As a general thing not more than six eggs are laid in a given pistil,— one on either side of each septum,— and frequently the number is smaller than this, so that even if they all hatch, which is not likely to be the case, there is rarely more than one larva to each tier of seeds, and consequently a fair percentage of the seeds are allowed to come to maturity. In the very succulent white ovary the puncture made in laying an egg is usually seen easily immediately after the ovipositor is withdrawn, and a rather large drop of clear sap not infrequently exudes from it within a short time.

Having withdrawn the oviduct, in doing which she moves up so that her head is about level with the stigma, or even before this organ is entirely freed, the moth usually proceeds to pollination; but it is not infrequent for two eggs to be laid between each two visits to the stigma, and, owing to her peculiar alertness, she appears to be even more easily frightened into omitting pollination than are the other species of Pronuba. Standing with her head at about the height of the stigma, with the short tongue projecting out in front, she uncoils her long tentacles from the compact mass of pollinia, — which she carries similarly to the other Pronubas, — only that small part of her burden which adheres to the bases of the tentacles being removed from it, and, raising her body on tiptoe, she very slowly saws the tentacles back and forth across the top of the stigma, generally following one of the three shallow grooves, and very carefully working their slender tips into the more or less gummy exudation over the central depression. Sometimes the operation is interrupted long enough to admit of the tentacles being coiled back against the load of pollen and again extended; but the curious manner in which her head is held back from the stigma as a rule prevents any of the main load from reaching even the marginal papillæ.

On first witnessing this operation, I was impressed by the much slower motion of the moth than usual, and the evident care which she took to run the ends of the tentacles into the central depression of the stigma, which I then supposed to be solid; the subsequent discovery of the stylar canal, communicating with the ovarian cells, showed that it is into this narrow passage that she so carefully guides the tips of her tentacles with their modicum of pollen, and no doubt the abundant stigmatic secretion serves not only to foster the development of the nascent pollen tubes after pollination, but, wetting the tentacles, aids in the disintegration of her mass of pollinia. These, if really related to her work, would seem to have acquired their coherent structure as a means of facilitating their collection, rather



HESPEROYUCCA WHIPPLEI, VAR. GRAMINIFOLIA.

than as an adaptation to their removal bodily from the anther to the stigma as is the case in orchids and asclepiads, where, however, special means of secure attachment to the insect accompany this aggregation of the pollen grains into a large mass.

As in the other capsular Yuccas, the pedicel of the fertilized flower soon becomes erect, and the ovary shortly begins to enlarge and assumes a bright green color. Owing to the injury inflicted in piercing its wall, the part immediately about the puncture does not take a very active part in this growth, and a cross section here shows a decided difference in size between the punctured and unpunctured half cells of the ovary, and, as the enlargement of the capsule continues, a decided pit appears, mostly of a darker green than the surrounding parts.

H. WHIPPLEI, var. GRAMINIFOLIA, (Wood). (Pl. 13, 23).—What I take to be this form, is the common Spanish Bayonet of San Bernardino, beginning near the foot-hills north of the city and extending up the smaller cañons and upon the mountain sides to an elevation of 1000 feet or more, and, in the Cajon Pass, reaching up toward Cajon Station, where the steep ascent of the pass begins. Recent notes from Dr. Yates, of Santa Barbara, show that a plant of the general character of this variety occurs in the mountains above that city, in addition to the typical *Whipplei;* and it appears to pass eastwards from the San Bernardino region, though I am not in possession of detailed information as to its distribution outside of the limited area between San Bernardino and the foot-hills north of that city. The plants are very abundant around the Arrowhead Springs, where the type of *Whipplei* does not occur, and I was able to make a rather careful study of them there shortly after the middle of April, when they were just coming into bloom, as well as a month later, when their flowering period was nearly past; and, still later, in company with Mr. S. B. Parish, I had an opportunity to drive over the principal part of the valley covered by this form, at a time when its

pollinator had almost completely disappeared, though some spikes were yet blooming.

In aspect, this variety differs from the typical *Whipplei* of the mountains in not being cespitose, and in its thinner, quite flexible, often broader and longer leaves. Its flowers are similar to those of the type except that they are commonly more or less brown-purple, and they are as variable in form. All about Arrowhead, at the time of my first visit, there were evidences of the work of a Pronuba in last year's capsules, which were very abundant, and I consequently expected to be able to study the work of *P. maculata* in the opening panicles. I was, however, surprised to see that the only Pronuba found on the plants of this vicinity, though possessing the usual *maculata* structure, was of a beautiful jet black color, and, with the exception of a single specimen, in which the thorax was dingy white, this proved to be the case with the thousands of moths seen or captured about Arrowhead and in the valley to a point near Irvington. I have called this melanic form *P. maculata*, var. *aterrima*.*

The females of this black Pronuba rest upon the ovary with their heads toward the stigma, precisely like the typical *maculata*, while the males also commonly stand upon the petals. Like the maculate moths, they are very alert, and quite ready to drop from the flower and take wing when disturbed. They are also active during the day, the males, especially, running and flying from flower to flower in quest of their mates; and copulation is seen within the flowers at all times of the day.

The collection of pollen was witnessed several times,

* *Pronuba maculata*, var. *aterrima*, n. var. Characters of the species, but the chitinized parts smoky brown, and the scales of a dead black color throughout, or a few pale ones near the tips of the primaries.—Living as a larva in the forming seeds of *Hesperoyucca Whipplei*, var. *graminifolia*, the flowers of which are pollinated by the female imago. In the foothills immediately north of San Bernardino, California, April, 1892. Types deposited in the Entomological collections of the National Museum, the Agassiz Museum and the California Academy.

under a cloudless sky, the first time at about noon. Flying into a flower, the moth runs about the bases of the stamens after the manner of other species, then quickly clambers upon the inner side of a filament, and, with the tentacles extended over the pollinia, drags first one and then the other out of the anther cells, pressing them together under the throat, and subsequently compacting the mass together much as *yuccasella* does the powdery pollen of other Yuccas, so that the ball finally consists of as many as ten or a dozen pollinia. So quick and energetic are the motions by which the pollinia are removed, that the stamens are often shaken quite violently, as I have before noted in the more nervous attempts of *yuccasella*. Oviposition and pollination, which were repeatedly witnessed, are performed exactly as by the maculate moth, the very slow movement in the latter operation being quite as striking.

The relationship of the Yuccas to one another and to their pollinators, the Pronuba moths, would be far more intelligible if we could trace their history back even a short distance into the later geological time, because as Yuccas and Pronubas both are undoubtedly of recent origin; but as was pointed out in the Third Report of the Garden, this is as yet impossible, since no certainly identifiable Yuccas exist in even the latest deposits, though plants bearing more or less resemblance to them occur far back in the geological epoch. In his paper so frequently referred to in the foregoing pages, Professor Riley has called attention to the ancient type of vegetation represented by the tree Yuccas. This is particularly true of *Y. brevifolia*, which in aspect resembles restorations of the Carboniferous *Lepidodendron* more nearly than any other form of recent or fossil tree with which I am acquainted. The other arboreous Yuccas are more like the Dracænas in habit, but the latter also belong to an antiquated type.

Though no single species extends across the continent,

the Yuccas occur in practically unbroken continuity from the Atlantic coast in the vicinity of Fortress Monroe to Florida, and across the Southwest and Mexico to California in the neigborhood of Monterey, *Y. glauca* reaching well up on the upper Missouri River, and *Y. baccata* following the Rocky Mountains northwards into southern Colorado. From this it may be inferred that they have become specifically differentiated at a comparatively recent date, an inference which is supported by the fact that notwithstanding various dissemination contrivances which may be held to be of still later acquisition, all of the species except the distinctively West Coast *brevifolia* and *Whipplei* may be broadly classed under the same type. The occurrence of so many species of the same floral type, and of what may be called modern habit of growth, over a common geographical area in the southern part of the continent, while the apparently ancient *brevifolia* is restricted to the desert region in or adjacent to California, and the seemingly more highly differentiated Hesperoyuccas occur only in the mountains near the latter region, though each has its specific *Pronuba* quite different from the one associated with the Eastern Yuccas, would lead one to surmise that the geological record, if it had been preserved, would show that the first of the Yuccas were of wide distribution, probably extending across the continent on the higher parallels while the northern climate was less rigorous than it now is, but receding to the south under the advancing glacial cold. Indeed it seems reasonable to suppose that the ancient type as represented in *brevifolia*, with an equally ancient type of *Pronuba*, has persisted in the Pacific region throughout, perhaps owing to the series of circumstances which have led to the preservation of the *Sequoias* in the same region,* while the more widely distributed species became differentiated and, with their pollinator, passed to the south under new conditions.

* See Gray, Presidential Address, Dubuque meeting American Association for the Advancement of Science,—Proceedings, xxi. 1.

All of the Yuccas agree in the possession of a general liliaceous type of flower, and in having compound pistils with a stylar canal and septal nectar glands. The latter characters, however, pertain to a considerable group of Monocotyledons, and evidently antedate the evolution of the Liliaceæ as an order.* If my view is correct, each of these characters came to Yucca in a fairly advanced state of development, from an earlier type of monocotyledonous plants. In *brevifolia* or its immediate ancestors, as well as in the eastern Yuccas, the stylar canal appears to have been extended and amplified at top through the marginal union of erect stigmatic lobes, so as to form the peculiar stigmatic chamber into which the pollen must be thrust in order to properly develop its tubes and fertilize the ovules.

Originally having spreading stigmas, we may assume that the progenitors of the Yuccas were slightly specialized entomophilous flowers, pollinated by hymenoptera, diptera or lepidoptera, which were attracted by the secretion of the septal nectar glands. With the consolidation of the stigmas, however, insects visiting the flowers for this nectar became inefficient pollinators, as may be seen when such insects enter the flowers of the existing Yuccas for the little nectar still produced; hence, with an economic reduction of the secretion of these glands, may have come an addition of their function to that normally borne by the stigma, in an increase in its secretion, so that the visitors, laden with pollen unconsciously accumulated while in the flower, should further visit the stigma on which some of their burden might be rubbed while they were feeding. During this stage of its evolution the plant appears to have proved especially attractive to some small moth, perhaps

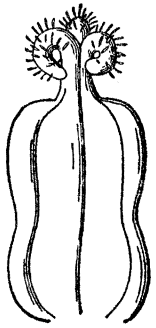
* For a stylar canal in *Agave* see Dañielli, Studi sull' *Agave Americana*, Florence, 1885, 59, pl. 10; George and Wittmack, Gartenflora, 1892, 273, f. 55, but incomplete. References to the principal papers on septal nectar glands are given in a short note by myself in the Bulletin of the Torrey Botanical Club, 1886, 135.

fond of nectar, and with phytophagous larvæ, which is to be regarded as the progenitor of the Pronubas and their close relatives of the genus Prodoxus, the history of which has been so well summarized by Professor Riley in the Third Garden Report. Whether the first Prodoxids were also pollen feeders, so that their mouth parts became accidentally laden with pollen between their visits to the stigma in search of its secretion, I cannot surmise. As my friend Dr. Lind has suggested, they may have learned to collect this substance and deposit it in the stigma through an instinct such as prompts the mud-dauber to place its prey about the point where its eggs are laid, or the bee to deposit honey and pollen where it can be used by the larvæ, as though its young were to be directly nourished by the pollen. At present, however, the act appears to be strictly voluntary, without food compensation, and entirely connected with the fertilization of the ovules. The fact that the septal glands of the several species still secrete at least a small amount of nectar may, as Riley believes to be the case,* depend upon the indirect utility of this secretion near the base of the flower in drawing insects other than Pronuba away from the stigma; or, as I am inclined to think, it may merely indicate that the abortion of the glands is not yet complete. The glands themselves need not be expected to disappear or to be reduced in size to an extent corresponding with their loss of activity under this latter supposition, for their persistence does not itself imply any drain on the forces of the plant, since they represent mere clefts in the connate walls of the carpels which have united to make the compound Yucca ovary. It is possible, however, that the rather abundant stigmatic secretion is not, as I have supposed, now being reduced from a still more abundant quantity that once served as true nectar, — and this assumption of a former nectariferous function of the stigma would be superfluous if Dr. Lind's theory were correct, —

* l. c. 110

since the Agaves, with an entirely different sort of pollination, possess an equally copious stigmatic secretion.

The Hesperoyuccas, represented by *Whipplei* and its variety, appear to have undergone a greater adaptation to general pollinators than the true Yuccas. Retaining the stylar canal and septal glands of the prototype, they have acquired a capitate stigma through the consolidation of the spreading lobes, the small stigmatic papillæ of other species becoming lengthened as a means of catching pollen adhering to visiting insects. On a few pistils, one of which is represented in the appended figure, the stigma is, in fact, separated into its carpellary



DIALYSIS OF HESPEROYUCCA STIGMA, × 2.

segments, each of which is strongly revolute. Similar instances of dialysis have also been observed in the true Yuccas, and these teratological specimens represent pretty nearly what I suppose to have been the original form of stigma in the ancestors of the Yuccas. The pollen grains may be assumed to have become somewhat viscid as a means of surer attachment to visitors which did not go deliberately to the anthers, and I am inclined to look on their agglutination into crude pollinia as a result of this, — perhaps intensified on the return of the plant to exclusive Pronuba pollination, — rather than an original provision for their bodily removal by other pollinators. These plants may, therefore, have branched off from the earlier Yuccas after a certain dependence on Pronuba had been formed, perhaps

acquiring their more general adaptations because of separation from Prodoxids, and readjusting themselves to their former pollinators on again coming within their reach; and I am disposed to think that this is the case, rather than to assume that the generalization antedates their first association with Pronuba.

The evolution of the Pronubas has presumably gone hand in hand with the adaptation of the Yuccas to their services in pollination, and has been sketched, in its essential features, by Professor Riley. It is interesting to observe that one species, *P. yuccasella*, accompanies the true Yuccas of the most differentiated type across the continent from the south Atlantic states to southern California (and undoubtedly the peninsula), and that, as the pollinator of *Y. baccata*, it occurs in California associated with *P. synthetica* and *P. maculata* and its curious black derivative, which pollinate respectively the archetypal *Y. brevifolia* and the greatly differentiated Hesperoyuccas, thus strengthening the inference that the latter two are primarily Pacific types, while *baccata* in its present form is an immigrant from the East, which has been accompanied by the common pollinator of the eastern species.

In a paper read before the American Association for the Advancement of Science at Rochester, in August, 1892, Professor Smith has shown that the curious tentacles used by the moth in pollinating the Yucca flowers, occupy a position similar to that of the palpifer on the maxillæ of other groups of insects, and so is disposed to homologize them with those parts. As Professor Cope has suggested to me, a fuller knowledge of the embryology of lepidoptera may show the general prevalence of similarly situated processes in the early differentiation of the maxillæ, and thus remove the only valid objection that I see to Professor Smith's conclusions, the isolated occurrence of these appendages in the group of lepidoptera. At present they are known in a developed form only on the females of Pronuba, and as rudiments on the males of that genus and

in the related genus Prodoxus. The occurrence of such rudiments in Prodoxus, however, is very interesting from an evolutionary stand-point, for it points to the inference that these moths are retrogressions from the Pronubas, rather than a nearer approach to the common parents of both.

The three types of fruit on which the primary classification of the true Yuccas rests, correspond with three modes of dissemination in the genus. About half of the recognized species have sweet, edible, pulpy fruits; two have indehiscent fruits similar to the preceding during their early development, but dry at maturity; and the remainder, including nearly one half of the true Yuccas, and the Hesperoyuccas, have dehiscent dry capsules. All of these fruits agree in their type of structure, as might be expected from the general uniformity in the parts of the ovary in the several species. In all of those I have been able to study during their development, the inner part of the ovarian wall, corresponding to the superior face of the infolded carpellary leaves, becomes more or less firm, the walls of its cells being thickened and deeply pitted, while the outer part is green and fleshy, and no doubt takes part in the assimilative work of the plant. In the Sarcoyuccas, this outer part becomes much thickened and quite succulent and sweet toward maturity, assuming a yellowish or purplish color and, in short, undergoing the usual ripening process of baccate fruits. The seeds, meantime, in most of these species, are immediately surrounded and protected by the firm inner layer previously mentioned, which suggests in texture and function the core of an apple, and in which the seeds rattle with considerable noise when the fruit is shaken. The pulp is easily removed from this core, which is usually shaped to the convexity of the thick seeds, so that when denuded it bears quite a strong superficial resemblance to a small ear of corn, a number of interspersed pale and undeveloped seeds, causing a mottling suggestive of

the "squaw corn" of the Indians. In *aloifolia*, where the pulp becomes almost black throughout, the very slight core also at length becomes pulpy. These fruits are well adapted to dissemination by fruit-eating animals, especially birds, the firm core suggesting that the pulp only is swallowed, the seeds being thrown away; but I do not know of any recorded observations on their dissemination.

The Clistoyuccas, with dry indehiscent fruits, comprise the curious tree Yucca of the deserts, *Y. brevifolia*, and a single eastern species, *Y. gloriosa*. Though frequent in cultivation, the latter is one of the least known Yuccas, and its fruit has been observed rarely. All that I can learn of it points to the conclusion that its fruit is of the Sarcoyucca type with rather thin seeds and suppressed development of the exocarp, suggesting a retrogression from *aloifolia;* but nothing can be said as to its dissemination. *Y. brevifolia*, however, differs from all of the other known species in having a very thick exocarp, corresponding to the pulp of the preceding group, but dry and spongy at maturity. The fruits of this species fall quickly after ripening, either by a distinct disarticulation or because of the brittleness of the pericarp at base, and their rounded form and very light specific gravity render them well developed "tumble fruits," and point to their dissemination over the dry sands of the desert by aid of the strong winds which prevail there, the seeds being liberated ultimately by the breaking of the fragile pericarp. Although *brevifolia* appears to be the least advanced of the Yuccas in its general development, I am disposed to look on this adaptation of its fruit to wind dissemination as a special acquisition, rather than regard it as representing the original type of Yucca fruit; yet, so far as the facts are known, it might equally well be held to be an advance on an earlier unspecialized fruit, or a retrogression from the baccate type.

In the capsular species, the green exocarp dries down to a rather thin layer at maturity, and the core, with this adherent film, dehisces through the true septa, and, for a

certain distance from the top, through the backs of the several carpels (Pl. 22). The seeds of all of these species are thin and flat and the capsules are erect, so that the adaptation to the scattering of the former, a few at a time, by gusts of wind, is that usual in capsular fruits of this kind. It is interesting to note that *Whipplei* and its variety, representing the aberrant group of Hesperoyuccas, possess the thin margined seeds of the capsular true Yuccas, but the capsules dehisce to the base in a loculicidal manner, that is, through the false partitions, the tough core-like tissue of which is arranged in a transverse lace-like structure (Pl. 23). Though dissemination depends on the wind in both cases, the seeds of the capsular true yuccas are lifted out of the pods by the wind dipping into the opened top of the cells, while in Hesperoyucca they are removed by puffs of air entering at the side through the lace work across the deep lateral clefts, in the manner beautifully described for *Lilium* in an anonymous article in the Bulletin of the Torrey Botanical Club, i. p. 46, and well known in the basket fruits of some Aristolochias, etc.

EXPLANATION OF PLATES ILLUSTRATING YUCCAS AND THEIR POLLINATION.

Plates 1-2, *Y. Guatemalensis*, flowering and fruiting plant at the Garden.

Plate 3, *Y. Schottii*, near Benson, Arizona.

Plate 4, *Y. australis*, near Sierra Blanca, Texas.

Plate 5, *Y. australis*, — a specimen from the same region, cultivated at the Garden.

Plates 6–9, *Y. brevifolia*, about Hesperia, California.

Plate 10, *Y. elata*, near Benson, Arizona.

Plate 15, *Y. elata*, descending axis, two and a half years from the seed, one-half size, — the principal growth made in the season when figured, (after Engelmann). — *Y. filamentosa*, germination, ×2.

Plate 16, *Hesperoyucca Whipplei*, at Summit, California.

Plate 17, *H. Whipplei*, var. *graminifolia*, at Arrowhead Springs, Cal.

Plate 18, *Y. aloifolia*. — 1, Flower, natural size; 2, pistil and stamens, ×2; 3, sections of pistil at points marked by dotted lines, × 2. *Y. Treculeana*. — 4, flower, natural size (after a drawing by Mrs. H. J Webber); 5, pistil and cross sections, ×2.

Plate 19, *Y. Guatemalensis.* — 1, Flower, natural size; 2, pistil and stamens, ×2; 3, sections of pistil at points marked, ×2; 4, fully grown but green fruit, natural size; 5, seed, ×2.

Plate 20, *Y. baccata.*— 1, Flower, natural size; 2, pistil and exceptionally long stamens, natural size; 3, pistil (the upper part in longitudinal section), and cross sections, ×2; 4, enlarging ovary, showing Pronuba punctures, natural size; 5, cluster of fruits, perforated by escaping Pronuba larvæ (after a photograph taken near San Diego, Cal., by Parker and Parker), reduced.

Plate 21, *Y. brevifolia.* — 1, Flower, at time of pollination, natural size; 2, pistil in longitudinal section, and cross sections at points marked, ×2; 3, *Pronuba synthetica*, ×3; 4, oviposition of moth, natural size; 5, head of laden ♀, ×10; 6, young larvæ in developing fruit, reduced one-half; 7, ripened but rather small fruit, from which the larvae have escaped, natural size.

Plate 22, *Y. filamentosa.*—1, Flower, natural size. *Y. elata.*—2, pistil and stamens, and cross sections of pistil, ×2; 3, dehiscent capsule, perforated by escaping larvæ, natural size. *Y. glauca*, var. *stricta.*—4, pistil and stamens, and cross sections of pistil, ×2. 5, *Pronuba yuccasella*, ×3.

Plate 23, *Pronuba maculata*, var. *aterrima.* — 1, Laden ♀, ×3; 2, head of same, ×10. *Pronuba maculata.* — 3, laden ♀, ×3, and venation of wings; 4, pollination. *Hesperoyucca Whipplei.* — 5, flower, natural size; 6, longitudinal section of pistil, and cross sections at points marked, ×2; 7, stamen, adnate to base of petal, ×2; 8, section of ovary punctured in oviposition, ×2; 9, small capsule, dehiscent through the false septa, natural size.

Unless otherwise stated, the plates were drawn by Miss Johnson, from photographs or studies by the author, or are reproductions of photographs.

Since the preceding pages were electrotyped, the paper by Professor J. B. Smith, on the maxillary tentacles of Pronuba, referred to on p. 222, has been printed in Insect Life, v. 161, Jan. 1893.

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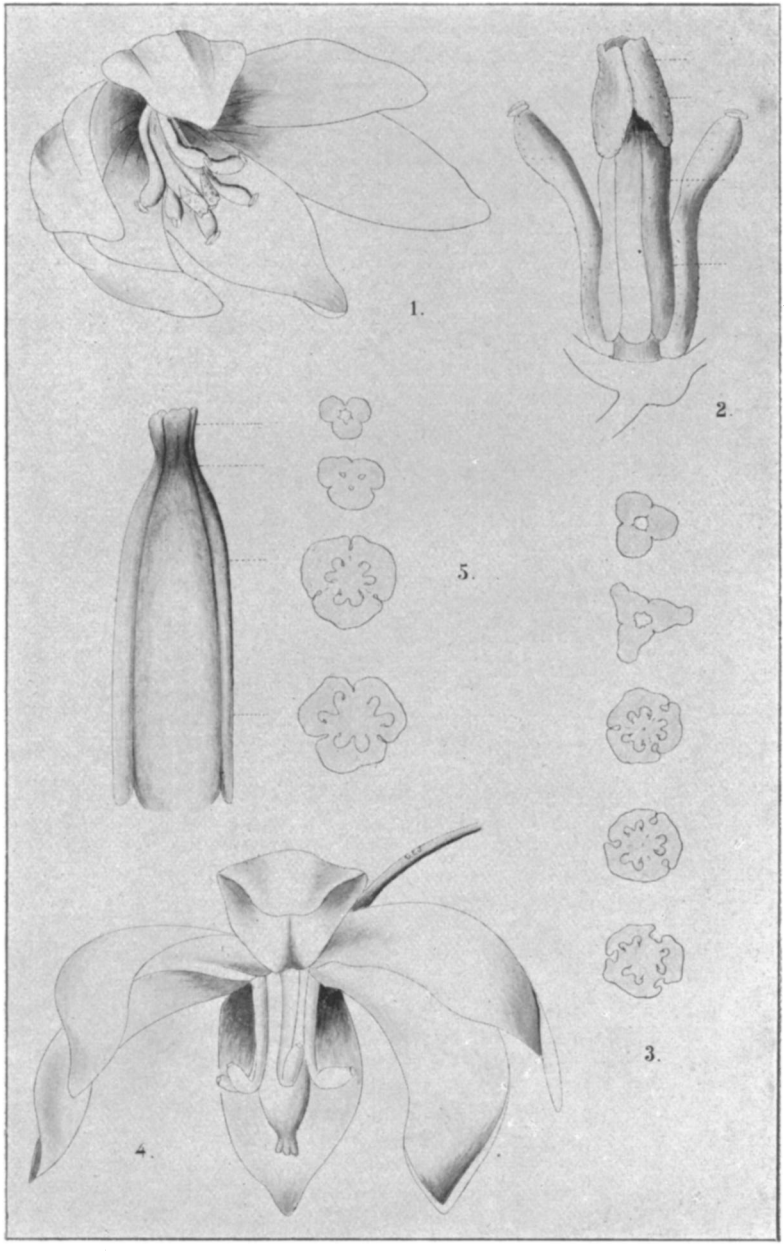
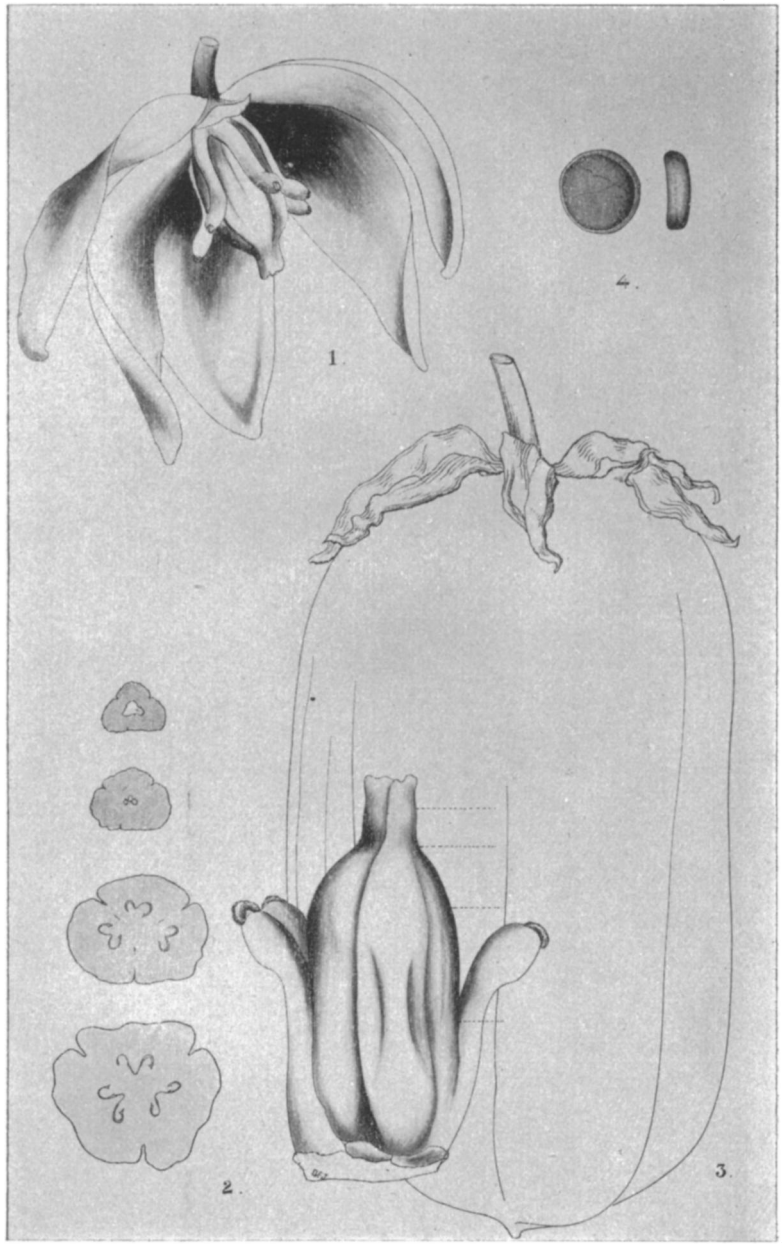
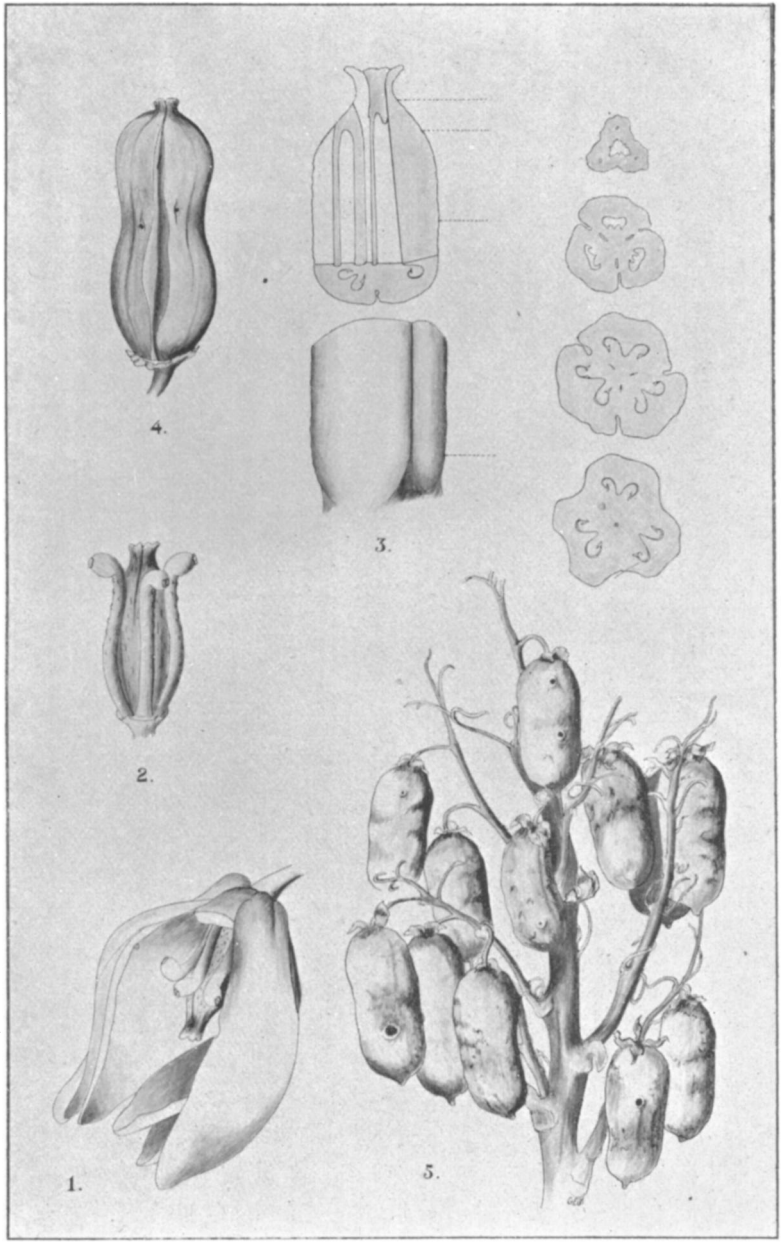


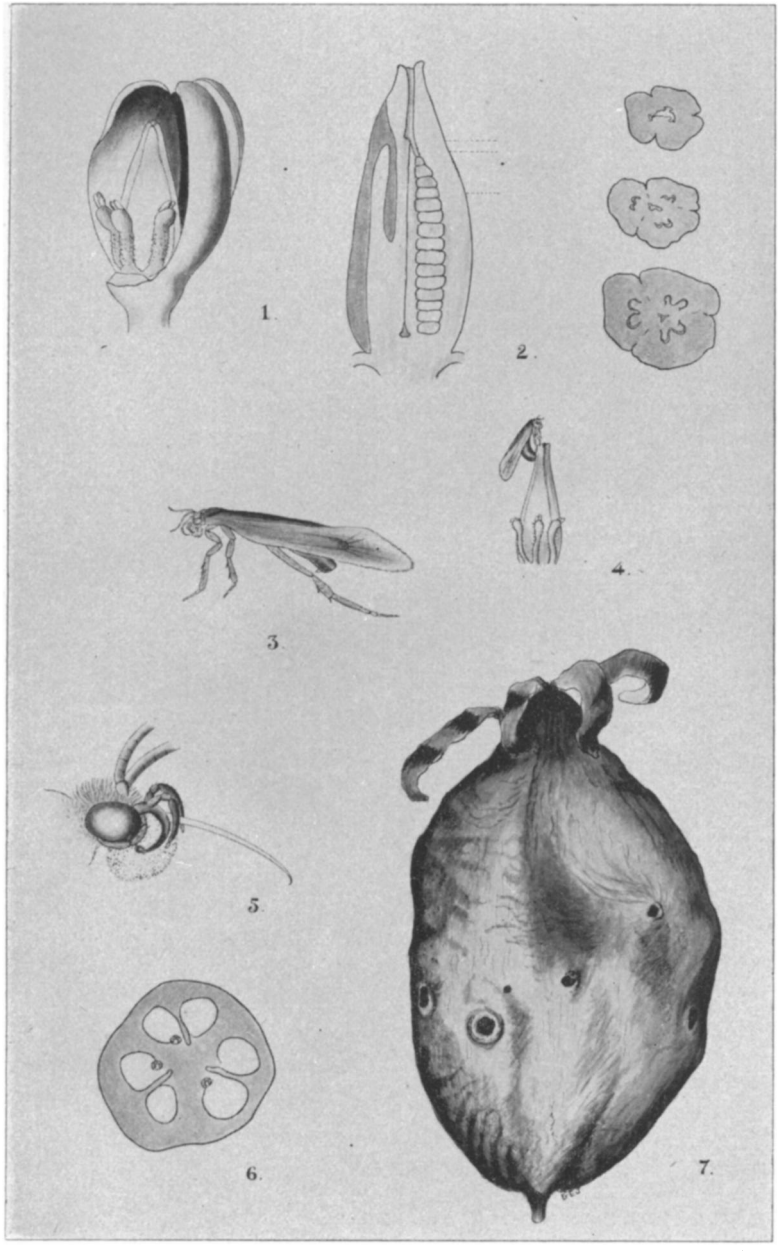
YUCCA ALOIFOLIA AND TRECULEANA.



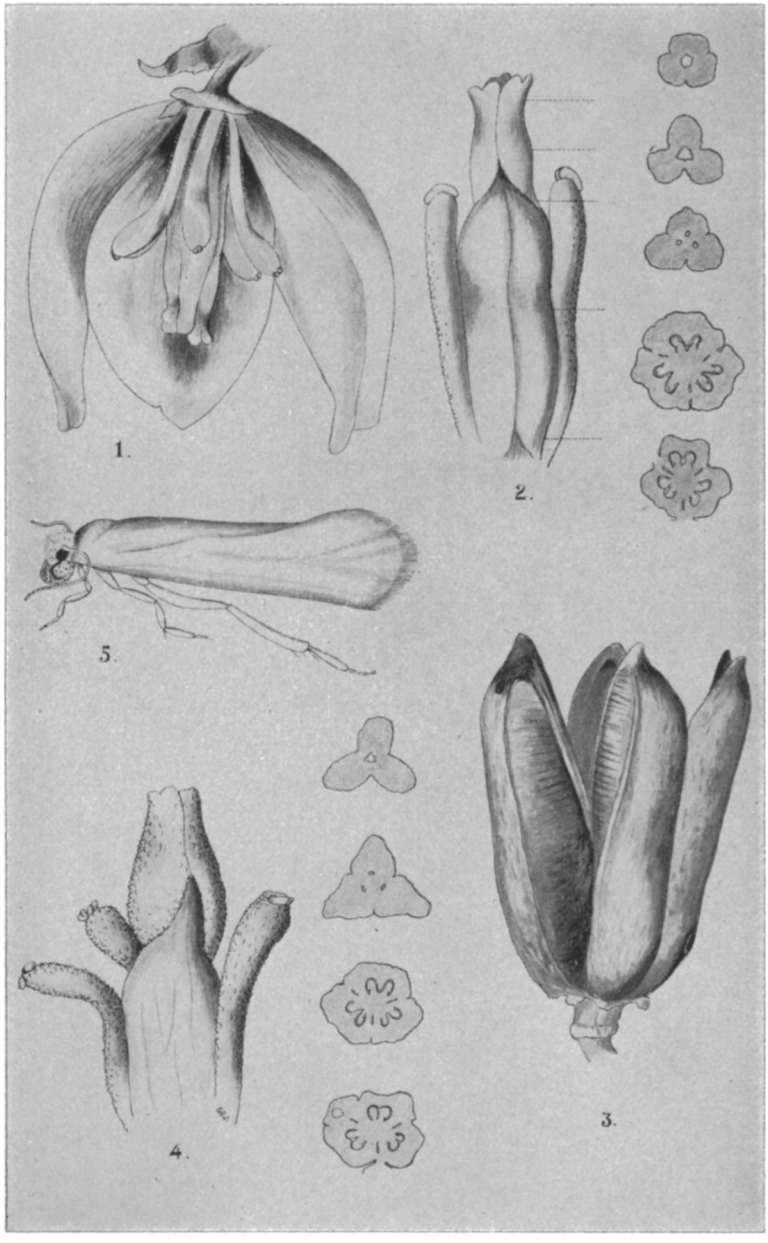
YUCCA GUATEMALENSIS.



YUCCA BACCATA.



YUCCA BREVIFOLIA.



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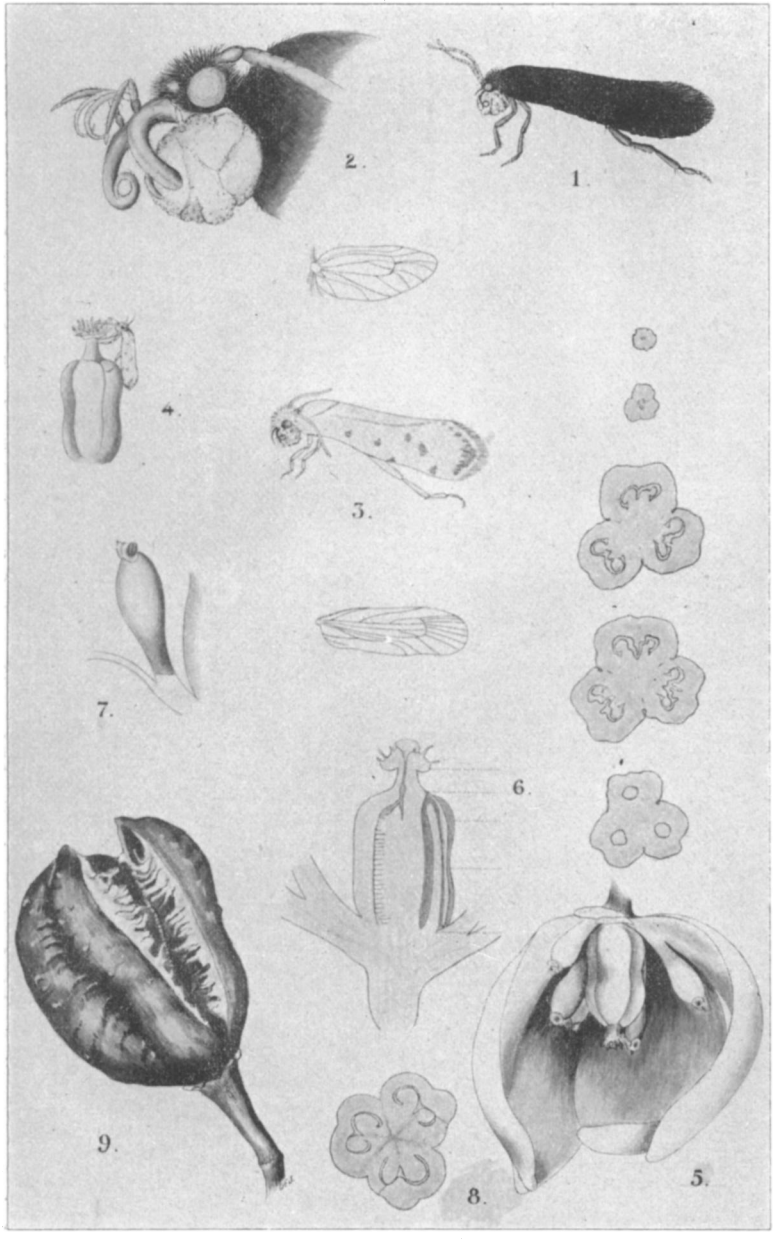

HESPEROYUCCA WHIPPLEI, AND VARIETY.